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MINNESOTA PLEISTOCENE HOMO AN INTERIM COMMUNICATION

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An area in North America about 1500 miles in diameter, of which Minnesota may well be taken as the center, has for several years jointly interested three departments of the University of Minnesota, namely: those of Anthropology, Botany and Geology. Interest centers primarily around the factors inherent in this area which seem to have been favorable for catching up and holding Glacial-Age man.

We have long believed man was in America before the close of the Glacial Age. The recent finding of so many members of the early Pleistocene genus, the new generalized *Sinanthropus pekinensis*, relatively so near the one-time ancient land bridge and so near the constant short water route between northeastern Asia and northwestern America has brought new stimulation to expectant open-minded students of glacial time in America.

Mindful of the existence and habitable conditions of the extensive driftless area lying in the adjoining states of Minnesota, Wisconsin, Iowa and Illinois, we have been on constant lookout for evidence of Glacial Man in Minnesota.

In pursuit of that end, a letter was written May 8, 1931, to Mr. C. M. Babcock, Commissioner of the Minnesota State Department of Highways, suggesting coöperation of Mr. Babcock's department with the University in the matter of reporting possible sub-surface discovery of human or animal bones, artifacts, or pieces of wood in the many cuts being made about the state during an extensive program of modern road building.

In response to this letter, on June 18, 1931, Mr. P. F. Stary, State Highway Maintenance Superintendent, stationed at Detroit Lakes, Becker county, phoned me that one of his road crews had found a human skeleton beneath the surface of a highway, south of Detroit Lakes. He asked if I could come up to investigate. As I was due to leave the University at once for summer archæological work in New Mexico, I arranged

with Mr. Stary to receive my colleague, Dr. Clinton R. Stauffer, geologist, and to deliver the skeleton to him. Dr. Stauffer visited the site on June 20 and 21, and brought the skeleton to my laboratory. Work in the field for the autumn quarter and full-time University work on my return prevented systematic study of the skeletal material until spring vacation beginning March 21, since which date time almost daily has been given to the study. The site of the find has also twice been redug, and I have obtained from the men present when the skeleton was found as complete a story as possible of its recovery. We have this story in detail, but I shall have time here for only a brief synopsis.

In June, 1931, on Minnesota Highway number 30, some three miles north of Pelican Rapids, in Pelican township of Otter Tail county, a maintenance crew working under Mr. P. F. Stary was cutting into the road-bed to lay drainage tiles the full length of a 600-foot frost boil. For an understanding of the story of the find, we must here note that this work was in a new section of the highway built in 1930 which cuts across an extinct glacial lake, the existence of which was first published by Dr. Frank Leverett in 1914. Horizontal laminated layers of the silt which filled this lake lie exposed abundantly in the long stretches of cuts made for this roadway. At Dr. Leverett's suggestion, we have named this lake "Glacial Lake Pelican."

A modern road grader hauled by a tractor dug into and through the highway surface from both its shoulders to its middle, making a shallow V-shaped cut the width of the twenty-eight foot oiled surface of the road-bed and two feet deep at the middle below the oiled surface. Mr. Carl Steffen was following the grader, when, early in the morning of June 16, the lower end of the blade, then making its lowest cut in the middle of the road-bed, exposed something white and shimmering in the yellowish gray silt. His attention was so arrested by the occurrence that he called Mr. Byron Doherty, operator of the tractor, to stop the grader. Mr. Steffen soon discovered that the foreign shimmering material was "clam shell crushed by the grader" blade. As he, with his fingers, cleared the silt away in which he found the shell fragments, he exposed the face of a human skull lying beneath the fragments. He then called Mr. Clarence Wright, the road boss. Messrs. Wright, Steffen and Doherty next saw partially exposed on the smooth-sheared surface of the silt what they thought was a piece of bone. This proved to be a broken dagger of antler.

Within the next hour after the skull was exposed, the skeleton was dug out, mainly by Messrs. Steffen and Eugene Russell, and removed to the side of the road. Seven men, members of the maintenance crew working on the frost boil, saw the skeleton in place while it was being dug out. They are: Carl Steffen and Byron Doherty whose part in the find has been told; Clarence Johnson, Carl Olson and Fred Sellman, truck drivers

Left Profile View "Minnesota Man" on Frankfort Plane.

Front View "Minnesota Man" on Frankfort Plane.

Occipital View "Minnesota Man" on Frankfort Plane.

hauling gravel to fill the excavated road-bed; Eugene Russell, truck dump man at the filling; and Clarence Wright, road boss on the job, who saw the skeleton from first to last and whose diary entry of that day fortunately documents the important discovery.

All men present agree that the skeleton lay on its left side with the head a little south of east. The face was turned somewhat upward so the right part of the frontal was uppermost in the silt. The legs were bent slightly backward at the knees. The upper legs were just noticeably flexed forward at the pelvis. The right arm was bent at the elbow so the forearm lay in front of the vertebral column while the upper arm was on top of the ribs and vertebrae. The left arm was beneath the ribs and was practically straight beneath or close in front of the body. A shell pendant was found with the skeleton among the ribs and vertebrae in the abdominal area. This pendant may have been hung from the neck, but I am of the opinion that it was attached to the girdle, perhaps as a pubic apron. There was no evidence about the skeleton that it was originally buried by man.

The cut at the spot where the skeleton was found is 7 feet and 6 inches deep from the old ground surface to the finished road-bed. The contour maps of this new section of the highway prepared by State Engineers before road grading began positively determine the sub-surface depth of the road-bed. The section of the road-bed beneath which the skeleton was found at a depth of 2 feet and 3 inches had not been disturbed by the original road builders in 1930.[1]

Mr. Wright told me that when he came to the spot where the skull was exposed by Mr. Steffen, he at once noticed and spoke of the smooth layers of silt lying from the middle of the road, where the grader had cut deepest, to the shoulder of the road, where the cutting began. The layers were exposed on the new sloping cut in the road-bed somewhat suggesting courses of shingles on a shed roof. Messrs. Doherty, Johnson, Steffen and Wright told me individually and together that they all saw the undisturbed layers of silt from beneath which the skeleton was later taken. All four of the men also told me that they talked of the skeleton at the time as probably that of "an old Indian" because it was found so deep in the earth.

Mr. Stary, coming down from Detroit Lakes, the morning of June 17, saw the skeleton by the roadside where it had lain since first recovered, and saying, "It is probably very important," ordered it taken to Headquarters' Camp, where it was later secured by Dr. Stauffer.

The first confirmation of the source of the skeleton was had May 7, 1932, when during several hours of cold, drenching rain, the reported site was redug for identification in the constant presence of Dr. Stauffer and myself. This redigging was done primarily by Mr. Steffen. Doctors George A.

Thiel, geologist, and Frederic K. Butters, botanist, University of Minnesota, also were at the site during much of the digging. All four of us were present when I picked out of the hole which Steffen was digging four silt-smeared fragments of the tell-tale mussel-shell. We may note that as the original fragments were over the fore part of the skull, the shell may well have been part of a head-dress.

Final confirmation of the source of the skeleton was made during the six days of August 2 to 7, 1932, inclusive, when under my supervision, by the labor of Mr. Lloyd A. Wilford, my assistant, and a field class of five students, the site was completely dug out. Mr. Steffen was in constant attendance as the representative of Mr. Stary. Drs. Stauffer and Thiel were at the digging several hours each day during the three days of August 3 to 5. During those days, they also investigated the immediate and neighboring environs checking glacial and geological data in relation to the age of the silt in which the skeleton was found. During our six days' work when all silt removed was scraped from its place in paper-thin sections by small hand trowels, 355 additional fragments of bone, antler, shell and turtle carapace were obtained. Pieces of antler, much broken and disintegrated, were found which do not belong to the dagger but two pieces of which at least are parts of an artifact. The pieces of turtle carapace may have been parts of an ornament or of a container.

At the time of the second redigging, we also put down a vertical trench in the northwest corner of the major excavation. This trench was dug to a depth of eight feet beneath the road-bed, the first 5 feet and 9 inches through layered silt. At that depth, white glacial lake sand was encountered upon which the water of the ancient lake had deposited its load of rock flour in the form of horizontal layers of silt. Thus, in the trench, there were 3 feet and 6 inches of laminated silt below the depth at which the skeleton was found.

Doctors Stauffer and Thiel will, in our final publication, give a detailed report of the geological significance of the find. I may say here that they are in agreement with Dr. Leverett that Glacial Lake Pelican is older than Glacial Lake Agassiz by about 2000 years, and is thus some 20,000 years old. They are convinced that the geological evidence compels the conclusion that the skeleton was in sediment of late Pleistocene origin.

We now turn to a brief consideration of the skeleton. It is remarkably complete. The original excavation secured bones of every unit anatomical part except wrist and hand, sternum, sacrum, patella, ankle and foot. Of those missing parts, there were found in the second redigging, bones of wrist and hand and sternum, and perhaps of the foot. Because of the nature of the silt matrix and the depth of the skeleton beneath the layered silt, no harmful alteration had occurred on the surface of the bones of the skull. They are ivory color, hard and smooth, and show without abrasion

every slight impression of blood vessel and convolution of brain. Although a few small parts of the cranium and upper face are missing from the skull, the only important part entirely unrepresented is the nasal bones. The jaws and teeth are in excellent condition, only the left upper lateral incisor is missing, having been lost soon after the skeleton was removed from the road-bed.

The indications are that the skeleton is that of a young woman. If the epiphysial criteria of the bones coördinate with those of modern persons, the age was seventeen years.

The skull largely shows distinct Mongoloid affinities, notable in the following characteristics: the moulding of the supraorbital and frontal region, the shallow supraorbital fossae, the low nasal bridge and the anterior jut of the malars.

The rounding of the borders of the nasal aperture is extraordinary and is strongly reminiscent of the condition seen in anthropoid apes. The extreme narrowness of the nasal aperture, together with its lack of lower borders, and with its rudimentary spine, stamps this skull as a most unusual specimen rarely paralleled in the crania of the same type. This narrowness of the nasal aperture is a feature quite unexpected in primitive American types.

The mandible is notable for the robusticity and thickness of the corpus, for the low and sturdy ascending ramus and the great gonial thickenings.

The supreme curved lines of the occipital, though faintly defined, rise very high thus making a huge planum nuchale. Between those supreme curved lines and the superior curved lines, there is a smooth area characterized by a double U-shaped groove (as U U) symmetrically disposed on either side of the median line. These appear to be channels for blood vessels. We have found no similar condition elsewhere in skulls or published data.

The interior of the skull shows a peculiar condition in the torcular region of the occiput. There a well-marked fossa occurs at the juncture of the left lateral sinus with the longitudinal sinus. The fossae for the occipital lobes of the cerebrum are strongly moulded.

The skull presents certain anomalies, but we have not time for their presentation.

We may say that aside from the geological evidences of the find, the skull is morphologically of a nature to compel its assignment as an early type of *Homo sapiens*. It is of a generalized Mongoloid type and not a specialized American type. For purposes of identification, we have named the type for which this skeleton stands the "Minnesota Man."

[1] Drs. Stauffer and Thiel made the depth measurements in terms of hundredths of a foot and found the depth of the skeleton to be 9.73 feet below ground level. For the sake of simplicity, I am calling this 9 feet and 9 inches.

THE FUNCTIONS OF THE OLFACTORY PARTS OF THE CEREBRAL CORTEX

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In reptiles and mammals the dorsal wall of the cerebral hemisphere which contains the superficial gray cortex is called pallium or mantle. In all amphibians and some fishes the corresponding part of the hemisphere can be identified as a pallial field or primordial pallium, even though superficial gray cortex is lacking or present in very rudimentary form. This identification is made on the basis of the position of this field and the anatomical arrangement of its nervous connections.

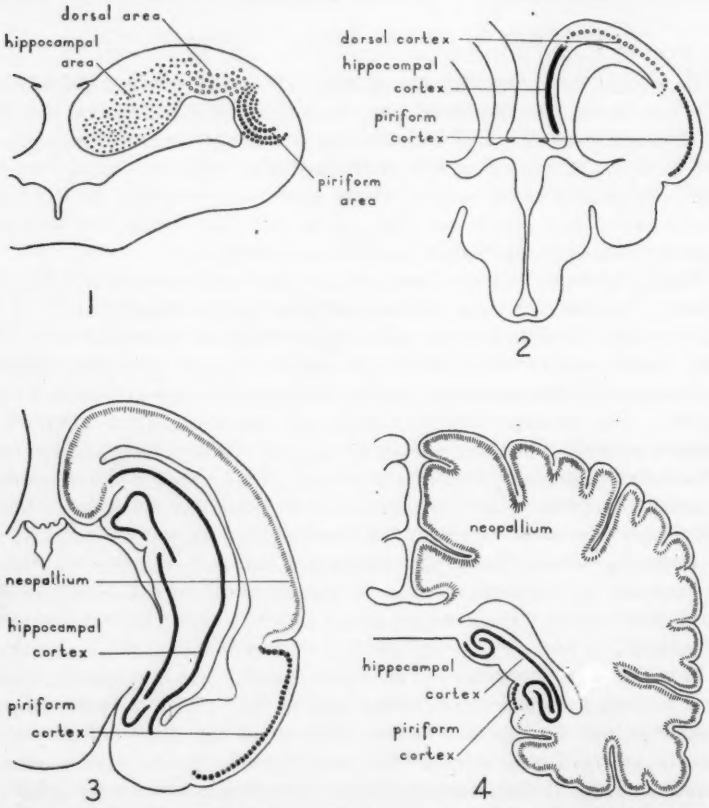
Below the reptiles (Fig. 1) the entire pallial field is dominated by the olfactory system, for large numbers of fibres spread throughout its mass derived either directly from the olfactory bulb or from an anterior olfactory area closely adjacent to the bulb. In reptiles (Fig. 2) well defined cortex is differentiated throughout the pallial field and this cortex again is dominated by the olfactory system, though the dorsal one of the three chief cortical areas receives a much larger proportion of non-olfactory fibres than does the corresponding area of amphibians. This cortex is of very simple pattern, consisting of one thin layer of cells which are arranged in three chief sheets or areas—medially the archipallium (hippocampal cortex), laterally the palaeopallium (piriform cortex), and between these the dorsal or "general" cortex which occupies the locus of the mammalian neopallium but has not attained the structure and connections characteristic of typical neopallium.

Between existing reptiles and mammals is a wide gap in pallial organization. In all mammals the olfactory part of the pallium is quite sharply separated from the non-olfactory neopallium and the entire pallial field is greatly enlarged and structurally complicated. In the lowest extant mammals (Fig. 3) the olfactory part of the pallium has already attained enormous size and complexity, and from this point onward in phylogeny it is very conservative, with little change in its organization except such as is incidental to the enlargement of the neopallium or the reduction of the peripheral olfactory apparatus in some species.

The neopallium, on the other hand, in primitive mammals is relatively small, in many cases being less extensive and less complicated than the olfactory pallium; but the mammalian series shows progressive increase in the size and complexity of the neopallium, which culminates in the human brain (Fig. 4) with upward of a hundred anatomically definable areas and a mass which makes up nearly half the total weight of the brain.

This rapid elaboration of the neopallium within the single Class of Mammalia is one of the most dramatic cases of evolutionary transformation known to comparative anatomy.

Why, within the mammalian class, does the olfactory pallium culminate



Figures 1 to 4.—Diagrams showing approximately the relative extent of the olfactory and non-olfactory pallial fields as seen in cross-sections of various vertebrate brains. Figure 1, Necturus, with entire pallial field olfactory (× 12); figure 2, the box-tortoise, Cistudo, with differentiated cortex, all of which is under olfactory influence (× 7); figure 3, the opossum, Didelphis, with olfactory cortex (hippocampus and piriform) more extensive than non-olfactory cortex (neopallium) (× 4); figure 4, human, with enlargement of neopallium and reduction of olfactory cortex (× 1/4).

in the lowest and earliest members and thereafter remain relatively stationary while the neopallium exhibits so amazing an enlargement and differentiation? Presumably the answer to this question is to be sought

in the significance of the pallium to the mode of life and to changes in the pattern of adjustment. Clearly the relative part played by the sense of smell in adjustments mediated by the cerebral cortex is very different in lower members of the series and in higher.

An analysis of cortical representation of the various sensory systems would seem to be an appropriate place to begin such an inquiry. First, it should be noted that the visceral, or interoceptive senses have meager cortical representation throughout the series; these internal adjustments are largely taken care of by subcortical nervous apparatus. The primary significance of the cortex, then, is to be sought in adjustments to external events as reported through the exteroceptive senses. Ancillary to these adjustments are the proprioceptive senses, which also have cortical representation.

The external environment is so much wider than the internal that effective adjustment to outside events requires a more or less accurate localization of the source of the stimulus. Appropriate response to a tactile contact or cutaneous pain can be made only if the locus of the stimulus is accurately registered in the central adjustor. For the senses of hearing and sight peripheral localization is even more important, for the source of the stimulus may be far removed from the body in any direction. The movable external ears of most mammals assist in this orientation. In primates the eye is the preëminent distance receptor, and here localization within the peripheral field reaches its ultimate refinement and central localization of the visual nervous apparatus is correspondingly precise.

The sense of smell stands in sharp contrast with these localizing exteroceptive senses. The organ of smell is both an exteroceptor and an interoceptor. For the latter function its central connections within the brain are intimately bound up with all of the other nervous apparatus of feeding, nutrition and reproduction, and the neurological pattern of these subcortical reflex connections is surprisingly constant from the lowest to the highest vertebrates. But smell is even more important as an exteroceptive sense, giving warning of enemies and other noxious things and guiding the animal to mates, food and other desirables.

The curious thing about these exteroceptive olfactory functions is that they are carried on very efficiently despite the total lack of any capacity for localizing the source of the stimulus within the olfactory sense itself. Odors may be discriminated in terms of quality and intensity, but they cannot be localized in space. If the source of an odor is to be determined, we must use some other sense—sight, hearing or direction of wind—or else we must move our own bodies to and fro to judge relative intensities of the odor.

Now all of these exteroceptive senses are highly developed in fishes and amphibians which lack well differentiated cerebral cortex; and of these,

in many of these animals, smell seems to be the dominant member. There is no evidence that the sense of smell of fishes differs essentially from our own and the close similarity of the central connections of the olfactory system of fishes with the subcortical olfactory connections of man points in the same direction. In view of the obvious importance of olfaction in feeding, mating and avoiding reactions and in view of its lack of localizing efficiency, it is evident that in these animals the olfactory reactions typically are not simple elementary reflexes but are ordinarily conjoined with other sensorimotor responses. What part do they play here?

The central connections of the olfactory nerve in all vertebrates are characteristically diffuse, widely dispersed and interconnected with one another and with other sensory systems in an intricate web of correlation fibres. From this complex the more specific olfactory pathways converge into a few final common paths, chiefly by way of the mammillary bodies and the interpeduncular nucleus. The main motor outflow from these centers is into the apparatus of mass movement (locomotion and the like), and these final common paths are the same as those of the other exteroceptors. Other olfactory outlets pass into the apparatus of various local reflexes, and here again they merge with the sensory systems which are the specific activators of these particular reflexes. There are some specific olfactory reflexes, like sniffing and nausea, but these are mostly visceral; when the organ of smell functions as a distance receptor the response is effected through final paths which are common to olfactory and other sensory systems and the pattern of response is determined by the conjoint action of all of these.

These arrangements suggest that exteroceptive olfactory excitations (leaving out of account here the visceral reactions) serve chiefly as activators of complex sensorimotor systems whose pattern of performance is determined primarily by other senses with sharper localization both physiologically and anatomically. The histological structure of the olfactory centers favors both irradiation and summation or intensification (avalanche conduction of Cajal) and it provides no recognizable apparatus adapted for the preservation of sharply defined local patterns of excitation such as is so characteristic of optic pathways and centers. Our own experience, too, gives many instances when faint odors call forth various non-olfactory activities, conscious or unconscious, without exhibiting any characteristic behavior patterns of their own. The quality of the stimulus apparently determines whether it is followed by a seeking or an avoiding reaction; but other details of the pattern of performance, particularly the localization of the source of the stimulus, are contributed by such other sensory excitations and bodily movements as may be in process.

The preceding discussion relates to subcortical activities which are common to fishes and men. It evidently has a bearing on the significance

of the olfactory cortex if we recall that in phylogeny the entire cortex was differentiated within and finally emerged from an olfactory field. In the lower Amphibia, where there is no differentiated cortex, the pallial part of the cerebral hemisphere can be readily recognized, and the whole of this field is clearly under strong olfactory dominance. Within this field well differentiated cortex appears in reptiles, and the whole of this cortex is again probably under strong olfactory influence. It is questionable whether anything properly called neopallium is present below the mammals, and, as already pointed out, in the lowest surviving mammals the olfactory cortex is more massive and far more highly specialized than the neopallium.

In the Amphibia, where cortex is not differentiated, there is no evidence that the olfactory influence upon one part of the pallial field is physiologically different (except in intensity) from that of any other part. Such incomplete differentiation of pallial fields as is apparent here has taken place under the influence of penetration of various systems of non-olfactory projection fibres into the pallial field, and this is probably true throughout all later phylogenetic stages. In Amphibia we see the beginning of penetration of exteroceptive systems of thalamic projection fibres into the pallial field, and in reptiles this is more extensive; but in neither of these cases is any region of the pallial field set apart as the exclusive receptive center for these fibres, nor within the thalamic radiations are the various sensory systems (touch, vision, etc.) segregated each with its own cortical projection center. This segregation and cortical localization does appear in mammals, and this marks the emergence of neopallium as contrasted with the "general cortex" of the reptilian dorsal pallial area.

The most primitive cortex, then, is an olfacto-cortex, that is, cerebral cortex in which olfactory connections and functions are well represented throughout its extent. But no degree of elaboration of olfactory apparatus alone has ever in any known animal given rise to cerebral cortex. Association is a characteristic cortical function, and this implies diversity in the things associated. Cortex does not appear in the pallial part of the olfactory field of any lower vertebrate unless and until several strong systems of non-olfactory projection fibres penetrate the pallium and have definite and separate localization within it. Association between these physiologically different pallial areas has value for behavior. These areas are different in their non-olfactory connections, even though olfactory connections are common to all of them. What, then, is the significance of these olfactory connections?

It seems probable that here, as in the subcortical field, olfactory impulses serve as activators of complex sensorimotor systems whose pattern of performance is largely determined by the non-olfactory members of the complex. This function, of course, is in addition to any specific olfactory

reactions that may be present. In reptiles there are from three to six incompletely separated cortical areas with different subcortical connections, all of which are under some olfactory influence and are structurally similar to the simplest olfactory cortex known in mammals. The supposed primordium of the neopallium at the anterior end of the dorsal area of "general cortex" is reached by thalamic projection fibres, and these so far as now known belong to the somesthetic system. If optic, auditory or other exteroceptive systems are represented, these have no localized cortical area of their own.

Such a cortex can have very little efficiency as an analyzer of experience. Probably all parts of it are activated by olfactory impulses, some more, some less. In the three chief projection areas they are combined with different aggregates of non-olfactory excitations, and all of these interact one with another through the associational apparatus. The net result of the total cortical activity would probably be in the main a differential inhibition or reinforcement of subcortical adjustments already in process with a minimum of either analytic or synthetic specificity within the cortex itself. In other words, this primitive type of cortex would tend to act as a whole to influence responses to external stimulation whose specific pattern is determined subcortically. There is doubtless some specificity of cortical reinforcement and inhibition, but so far as can be inferred from structural arrangement this can be only of very general sort.

In even the lowest of the mammals there is a tremendous advance. The neopallial field is well defined and within it are clearly localized somesthetic, optic and auditory areas, each with its own system of thalamic projection fibres, and there is a much larger mass of intrinsic associational apparatus. The olfactory cortex shows still greater advance, and indeed it has already reached the culmination of its differentiation. This differentiation shows an elaborate apparatus for summation and intensification of olfactory excitations and little evidence of patterns of cortical localization. Such histological localization as is apparent is chiefly at the margins of the olfactory field where neopallial connections are strongly developed and of different composition depending on the localization patterns of the adjoining neopallium.

In sharp contrast with this arrangement, the definite localization pattern of the neopallium indicates that this cortex can now perform the functions of an analyzer in simple situations. It can probably also initiate new patterns of behavior ("insight" of Köhler or "reasoning" of Maier); but this synthetic function is meagerly represented and moreover it is held in abeyance under ordinary conditions by the enormous preponderance of the olfactory type of cortex.

These inferences drawn from structural arrangements are supported by what experimental evidence we have of cortical participation in behavior

patterns of lower mammals, such as opossums and rats. Here there is evidence that the cortex exerts some relatively non-specific influence upon learning and remembering; and, in the simpler situations especially, this is in large measure independent of the localization pattern. The whole cortex seems to act as a differential activator or inhibitor. But this is not all of the story, for in certain types of experiment, and especially in more complicated problem situations, the cortical participation is of different type. The localization pattern enters into some of these situations, indicating that the analysis of peripheral experience by the sense organs is maintained up to the cortical level and here synthetically recombined in new patterns. This gives "insight." It is this synthetic function which is enlarged in higher mammals and this implies cortical representation of peripheral localization, so that the outer world is correctly and adequately mirrored in the inner (cortical) experience. This spatial representation of the outer world requires localization in space of the central apparatus, and this is what we find anatomically in the visual nervous pathways and centers preëminently. The experiments of Lashley and others show that cortical participation in the conditioning of visual habits is more definitely localized than of somesthetic habits like maze-running.

It is perhaps significant in this connection that in most of the experiments designed to test the part played by the cortex of lower mammals in learning the ablation operations involve only the neopallium, leaving the olfactory cortex intact or but slightly injured. Under these conditions that part of the cortex which is preëminently non-specific in its normal function is still acting in full efficiency. It is true that the neopallium also contains a large amount of non-specific tissue which is physiologically equipotential, but this tissue, unlike that of the olfactory cortex, is set within a matrix of physiologically specific and localized projection cortex. It will be interesting to find out just what happens to these adjustments to external situations—problem boxes and the like—when the olfactory cortex is wholly removed, and the hippocampal and piriform parts separately, with the neopallium left so far as possible intact. These are difficult, but probably not impossible surgical operations.

We have experimental proof that total destruction of both olfactory nerves impairs cortical efficiency in learning where smell is a factor in the process of conditioning, as, of course, is inevitable. But this operation sheds little light on other intrinsic functions of the olfactory cortex, for the associational connections of this cortex with the neopallium are very extensive and diversified and in an animal deprived of olfactory organs these connections are still intact. The "olfactory" cortex may exert a profound influence upon all neopallial activity even in an animal which is normally totally anosmic, as indicated by the preservation of well differentiated hippocampal cortex in the dolphin which has no olfactory apparatus.

The inferences drawn from these considerations are:

1. In exteroceptive adjustments the olfactory sense, lacking localization of its own, coöperates with other senses in various ways, including a qualitative analysis of odors and the discrimination between desirable and noxious stimuli, activation or sensitizing of the nervous system as a whole and of certain appropriately attuned sensorimotor systems in particular, with resulting lowered threshold of excitation for all stimuli and differential reinforcement or inhibition of specific types of response.

2. Tissue differentiation within the pallial field began in phylogeny with the penetration into this part of the primitive olfactory area of various systems of non-olfactory projection fibres, resulting in more efficient adjustments (both interoceptive and exteroceptive) to all situations containing olfactory excitation.

3. In the course of differentiation of the cerebral cortex the olfactory system plays the dominant rôle in primitive types, to be reduced to a subordinate position in primates as the neopallium is expanded and differentiated.

4. At all stages of cortical elaboration an important function of the olfactory cortex, in addition to participation in its own specific way in cortical associations, is to serve as a non-specific activator for all cortical activities. This is a generalized activity of primitive type acting on the neopallial cortex as a whole, lowering its threshold or increasing its sensitivity, or, in the case of noxious stimuli, exerting inhibitory influence.

This type of non-specific activity is one of the major functions of the olfactory cortex, though all parts of the neopallium also exhibit it to some degree. It comes to expression in overt behavior, learning capacity, memory, etc., as a differential influence upon other cortical and subcortical functions of those exteroceptive sensorimotor mechanisms whose specific patterns of response show well defined anatomical and physiological localization. Having no localization pattern of its own, it may act in two ways: first upon other exteroceptive systems whose localized mechanisms are adapted to execute adjustments where external orientation is demanded, and, second, upon the internal apparatus of general bodily attitude, disposition and affective tone, the "intimate senses" of Starbuck.

[1] This research was aided by a grant to the University of Chicago by the Rockefeller Foundation.

A PHYLOGENETIC CONSIDERATION OF THE OPTIC TECTUM

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It is not unusual in the consideration of the optic tectum to regard it as dominated on the afferent side by the optic tract. It cannot be denied that there exists a direct relation between the size of the eye and the development of certain layers of the optic tectum, but it is equally true that the tectum is a sensory correlation center and to a very considerable degree its size, and more particularly its lamination, evidences the relative variety and complexity of the non-optic afferent impulses reaching it from the brain stem and diencephalic region. But its function as a sensory correlation center is only one phase of its activity, since afferent impulses correlated through the interrelation of its neurons, are affected through efferent paths arising from certain of its neurons so that it becomes not only an important afferent correlation center but also an equally important efferent center, containing the upper neuron of the final common path.

On casual examination of the optic tectum of different vertebrate orders there would appear to be a wide variety of patterns, the apparent number of layers varying from two or three in certain urodele amphibians to approximately fifteen in reptiles and birds. In an endeavor to elucidate the structure of the optic tectum, one method of approach, adopted and developed particularly by the Spanish school, was to designate by number, numerically arranged from within out, cell and fiber layers. The application of this system of numbering to the tecta of different orders of vertebrates led to the use of the same numbers to designate widely divergent functional fields. According to the above indicated system of numbering there were described in the optic tectum of reptiles fourteen distinct layers. In recent studies, Huber and Crosby, with use of abundant reptilian material, containing series cut in several critical planes and prepared to reveal cell structure and arrangement, medullated and nonmedullated nerve fibers, were able to group these various layers into six strata, on the basis not only of morphology but of morphology and function, and they regard these six strata as presenting a fundamental pattern, present potentially or with full expression or again with slight regression in all vertebrate tecta. These strata we have named:

1. Stratum opticum.
2. Stratum fibrosum et griseum superficiale.
3. Stratum griseum centrale.
4. Stratum album centrale.

5. Stratum griseum periventriculare.
6. Stratum fibrosum periventriculare.

Following a functional pattern these layers are enumerated from the periphery toward the ventricle, contrary to the older numerical designation which was from the ventricle outward.

The stratum opticum, as its name implies, is composed of the main bundles of the optic tract fibers which enter the optic tectum along almost its entire ventral circumference and pass dorsalward. Certain of these optic fibers synapse with the dendrites of tectal cells close to the stratum of optic fibers, while others penetrate to various levels of the underlying stratum and there come into synaptic relation with the dendrites of cell bodies situated in all of the deeper cell layers. The stratum fibrosum et griseum superficiale, as its name implies, consists essentially of alternate fibrous and cellular layers of which the former represent in part regions of synapse and in part pathways of afferent fibers, while the cellular layers are composed of neurons receptive to incoming impulses. The incoming impulses, other than the optic, are tactile, pain and temperature impulses from the spinal cord by way of spino-tectal paths, tactile, pain and temperature impulses from the head by way of trigemino-tectal paths from the cutaneous centers of the medulla oblongata, and auditory impulses from the cochlear centers of the bulb in part at least by way of the nucleus isthmi. These receive important additions from impulses carried by certain commissural systems and by fiber bundles from the diencephalon particularly the dorsal thalamus, and from the pretectal and subtectal centers. These connections indicate that the stratum fibrosum et griseum superficiale is a main receptive area of the optic tectum and that within its confines occurs a correlation of optic and non-optic exteroceptive impulses, in which correlation, however, neurons of deeper strata participate. The degree of layer differentiation in the stratum fibrosum et griseum superficiale correlates directly with the volume and the relative importance of the non-optic impulses in the various vertebrate orders. Within the stratum griseum centrale lie the cell bodies of neurons, the neuraxes of which constitute efferent paths. Such neurons send their major dendrites toward the periphery of the tectum, where they come in part into direct synaptic relation with incoming optic and non-optic fibers, and in part receive impulses after these have been subjected to recombinations in the stratum fibrosum et griseum superficiale. Certain secondary ascending fibers appear to terminate directly within this stratum. The neuraxes of the neurons of the stratum griseum centrale, with certain exceptions, reach the stratum album centrale, composed of the major efferent pathways from the tectum to lower centers Collaterals turn into the stratum fibrosum et griseum superficiale for reinforcement, as do neuraxes of other

neurons of the stratum. Internal to this stratum is found another cellular layer, the stratum griseum periventriculare, which varies greatly in thickness and layer differentiation in the various reptiles, and presents still wider variation in the different vertebrate orders. This stratum consists of neurons possessing long dendrites which extend toward the periphery and shorter dendrites which are directed toward the ventricle. The longer dendrites form synaptic relations which are comparable to those of the stratum griseum centrale, while the shorter dendrites receive impulses from the periventricular system of fibers. This periventricular system, which phylogenetically considered is a very old system, and is present with varying degree of expression in all vertebrate orders, is highly developed in reptiles. It is composed of fiber fascicles, many of which are unmedullated, which arise from the preoptic and hypothalamic regions (thus presumably from olfacto-visceral centers) from dorsal thalamic centers (largely somatic) and from midline tegmental gray, and in entering the tectum course between the ependymal layer and the stratum griseum periventriculare. These are reinforced by important connections from the inferior colliculus, which constitute an acustico-optic system. These acustico-optic fibers and the periventricular system together constitute the major part of the stratum fibrosum periventriculare, in which stratum they come into synaptic relations with the short dendrites of the neurons of the stratum griseum periventriculare. Therefore, it is evident that the neurons of the stratum griseum periventriculare correlate a great variety of impulses, serving as efferent centers since many of their neuraxes enter the stratum album centrale, which has been characterized as composed of the chief efferent pathways.

This pattern as found in reptiles expresses structurally a functional differentiation, as is evident by a comparison of the reptilian optic tectum with that of amphibians on the one hand and with mammals on the other. As presented in the literature (Herrick), the urodele tectum consists essentially of an inner cellular layer and an outer fibrous layer of which the more peripheral portion is composed of optic tract fibers, representing a fundamentally primitive stage both in phylogeny and in ontogeny. The dendrites of the neurons of the central gray extend toward the periphery, where they come into synaptic relation with optic and other incoming paths. The neuraxes, which often have dendritic origin, leave the tectum just superficial to the cell layer, between it and the incoming paths. In higher amphibians, as in the frog, there is to be noted a step of further differentiation in that certain neurons of the central gray have migrated toward the periphery to form somewhat indistinctly delimited layers among the fiber bundles. Thus there is here evidenced the beginning of a stratum fibrosum et griseum superficiale and a stratum griseum centrale, a development which can be correlated with the greater development and particularly

with the greater specificity of the afferent tectal pathways resulting in a relatively greater size and functional significance of the optic tectum. Moreover, the efferent pathways in the optic tectum of the frog arise and course as they do in the reptiles among and internal to a part of the cells giving origin to them, so there is a morphological differentiation into a stratum griseum centrale, a stratum album centrale and a strateum griseum periventriculare, for the more centrally placed neurons of the cellular layer are concerned particularly with the entering periventricular system thus constituting the functional beginning of a periventricular gray stratum.

The contrasting of the tectal development as noted in the urodele with that as described for frog and reptiles serves to illustrate the great advance in morphologic differentiation in the latter forms. The high degree of morphologic differentiation can be correlated directly with the great increase in the functional significance of the optic tectum of reptiles, constituting this area, with the closely associated dorsal thalamus, the greatest sensory correlation center of the reptilian brain, amply documented by the richness and variety of fibers constituting its efferent paths. The most obvious morphologic change noted on comparison of the lower amphibian and the frog and reptilian tecta, is the separation of the central gray layer of the lower amphibians into a stratum griseum centrale and a stratum griseum periventriculare with the interposition of a stratum album centrale in frogs and reptiles. This is explainable in part on the supposition that further migration of cells toward the incoming pathways in response to neurobiotactic influences has occurred, thus submerging the layer of efferent fibers, in part added to by the actual turning in of neuraxes, as evidence by the looping of these in the form of shepherd's crooks, so clearly seen in chrome-silver preparations. The degree to which this more central position of neuraxes has been attained varies as we pass from the frogs and more generalized to the more specialized reptilian forms, for in the turtle a considerable portion of the efferent fiber paths still course in the stratum griseum centrale, while in certain of the lizards, in the main, they are more deeply concentrated in the stratum album centrale. The presence in reptiles of a well differentiated stratum fibrosum periventriculare is to be correlated with the high degree of differentiation of the periventricular system in these forms, representative of a high degree of correlation of the optic tectum with the midline mesencephalic and diencephalic centers and the mesencephalic auditory centers, in the main a system of ventro-dorsal correlation.

In the bird there is to be noted a further amplification of the pattern observed in reptiles, expressed largely in the increase of the number of layers or zones within the stratum fibrosum et griseum superficiale, which constitutes a major layer for the reception of impulses. Morphologically

considered the acme of development as regards relative size and differentiation is reached in the reptilian and the avian tecta. It is worthy of note that almost the same degree of tectal differentiation is attained in certain of the bony fishes, where again the optic tectum constitutes a dominant sensory correlation center.

On comparison of the mammalian optic tectum with the reptilian optic tectum, the former on casual examination appears as less highly differentiated, and the degree of differentiation in mammals decreases as one passes from the lower to the higher mammalian forms. Eight layers were enumerated by Tsai in a relatively recent contribution on the optic tract and the optic tectum of the opossum, and this enumeration did not include a periventricular fibrous layer. The layers thus indicated are homologized easily with the strata described for reptiles. The observer's innermost cell layer corresponds to our stratum griseum periventriculare, the overlying fiber layer to the stratum album centrale, the following cell layer to the stratum griseum centrale and the succeeding fiber and cell layers, exclusive of the superficial optic stratum, and his stratum zonale, with the associated gray, are components of our stratum fibrosum et griseum superficiale. As one progresses from marsupial to rodents and carnivores and to the higher primates the six fundamental strata are still represented, but the relative development and differentiation of the several strata varies as one passes from lower to higher forms. The differences in development are exhibited more particularly in the differentiation of the two receptive layers, the stratum fibrosum et griseum superficiale and the stratum griseum periventriculare with its associated stratum fibrosum periventriculare.

In human the description of the optic tectum is based largely on Weigert preparations. The following layers are very generally recognized and are here enumerated from without inward: 1, a stratum zonale; 2, a stratum griseum or cinereum; 3, a stratum opticum; 4, a stratum lemnisci, containing cells as well as fibers; 5, a stratum profundum, likewise containing gray and white, and, internal to this layer, the scattered cells of the mesencephalic root of the fifth nerve with periventricular gray. The most obvious difference between the primate and the reptilian tectum consists in the relative position of the stratum opticum and this difference is only relative, for while in many reptiles the optic tract lies close to the periphery in others, as in the turtle, it is separated from the surface by a zone containing here and there a few cells on its inner surface, forming thus a potential stratum zonale. In mammals, as seen in the opossum and on up through primates, the stratum opticum, which belongs to the afferent systems of the tectum, lies relatively deeper within the main receptive layer so that certain of the afferent fibers, largely cortico-tectal and thus new in mammals, and the receptive gray lie superficial to the optic stratum,

constituting the stratum zonale and the stratum cinereum of mammals. The stratum lemnisci of mammals, with its gray and fiber components is a direct representative of the main portion of the stratum fibrosum et griseum superficiale. The stratum profundum with its outer layer of gray and its inner layer of white constitutes respectively the stratum griseum centrale and the stratum album centrale. The stratum griseum periventriculare and its associated stratum fibrosum periventriculare are present certainly in higher mammals, the former being constituted in man by other cells and the cells of origin of the mesencephalic root of the fifth nerve, and the latter, as far as evidence exists at present, being limited to relatively few scattered fibers. Therefore, it is evident that the postulated six fundamental tectal strata are present in mammals including man although somewhat modified in accordance with functional changes.

The foregoing account emphasizes two aspects of tectal phylogeny. One of these concerns its development according to a fundamental pattern; the other is concerned with the variation in correspondence with its rôle as a correlation center and its relationship to the sensory correlations of the brain as a whole. The *raison d'être* of this fundamental pattern as well as of its variation is to be sought in its dual activity, on the one hand serving as a sensory correlation center and on the other hand as a discharge center for efferent impulses. Stratification, simple or complex, is a morphologic expression of the subdivision into afferent and efferent centers. The main efferent (but also correlative) center and fiber tracts occupy the more central portion and thus separate a superficial receptive correlation layer from a deep or periventricular layer, primarily receptive and correlative but also efferent in function. The trend of development as one passes from amphibians to reptiles and birds is toward an increase in the richness and complexity of the afferent sensory impulses; optic, tactile, pain and temperature impulses from the body and the head and correlated somatic sensory impulses from the dorsal thalamus of the same and opposite side, together with rich intertectal, pretectal and subpretectal connections, so that the tectum with the intimately related dorsal thalamic centers become the main sensory correlation center of the brain, overshadowing in richness of correlation and degree of morphologic differentiation the developing cortex in these forms. The alternating layers of gray and white within the receptive area undoubtedly permit a localization of impulses within this area. The ventrodorsal correlation systems, as represented in the periventricular fibers, and the acustico-optic fibers, carrying in auditory impulses from the inferior colliculus, were described as coming into relation with the neurons of the periventricular gray. These neurons, through the spread of their dendrites into the stratum fibrosum et griseum superficiale, serve to correlate within themselves optic, tactile, pain and temperature impulses, with auditory impulses and with the impulses brought in through

the periventricular system, which in part as least are olfacto-visceral in character. Since the periventricular layer and fiber paths which influence it are large in the reptilian tectum, they must be regarded as of distinct significance in any consideration of it as a sensory correlation center. The high development and differentiation of both of these receptive layers in reptiles and in birds is morphologic evidence that in these forms the tectum has reached the peak of its development as a sensory correlation center. The efferent paths in the reptilian and avian tectum are also well developed, discharge being made to diencephalic, tegmental, cerebellar and bulbar centers, with few if any tecto-spinal paths. Of particular interest are the tecto-thalamic connections, for the dorsal thalamus receives at best few lemnisci fibers and is dependent for its development upon the various sensory impulses which reach it by way of bulbo-tectal and tecto-thalamic paths, the development of the dorsal thalamus going hand in hand with the development of the tectum in these forms.

In the mammalian brain the highest sensory correlation centers are found in the cerebral cortex, which, with the exception of the olfactory cortical areas, interrelate impulses brought into the cortex from the dorsal thalamus, consequently in all mammals there are to be found thalamo-cortical paths, which increase in number and complexity as one passes from lower to higher forms. This increase in the dominance of the sensory centers of the cerebral cortex is associated with a gradual decrease of the optic tectum as a dominant sensory correlation center. In causal relation to its decreasing importance as the major sensory correlation center are to be emphasized changes in its fiber relations. An increasingly greater number of optic tract fibers terminate in the metathalamic lateral geniculate nucleus, so that in man, at least, the optic tectum has chiefly such direct optic tract fibers as mediate light reflexes. However, visual impulses reach the optic tectum after a synapse in the dorsal nucleus of the lateral geniculate body, through the peduncle of the lateral geniculate. And further, the ascending sensory pathways in crescendo from lower to higher mammals in the main skirt the tectal region in order to reach their major nuclei of termination in the dorsal thalamus, contributing in their course small bundles and in certain cases collaterals only to the main receptive stratum of the optic tectum. With the gradual loss of its function as a necessary relay station in the path of ascending sensory impulses to the dorsal thalamus there is noted a gradual decrease of tecto-thalamic and thalamo-tectal fibers, the only clearly recognized exponent of these systems in man being found in the peduncle of the lateral geniculate and certain commissural systems. This decrease in the afferent systems to the tectum is evidenced structurally by a relative reduction in the differentiation and size of a part of the outer receptive layer, the stratum lemnisci. There is a shifting inward of the optic tract so that the stratum fibrosum et griseum

superficiale, represented in amphibians and highly developed as a single stratum in the reptilian and avian optic tecta, is differentiated in mammals into a superficial portion to which in man the name stratum zonale and stratum cinereum are generally applied, and a deeper portion commonly known as the stratum lemnisci. Consequent to a decrease in the afferent systems there is noted a decrease in the tecto-thalamic paths.

The efferent paths to motor centers carry progressively longer fibers in passing from lower to higher forms, so that in man tectospinal paths have been traced to at least the middle of the spinal cord. Thus in this sense the efferent systems of the optic tectum are more efficient in higher mammals and in man than in the lower mammals. The marked reduction of the stratum periventriculare fibrosum in higher mammals and man appears to be associated in part at least with the reduction of the periventricular fiber system.

It must be evident from what has preceded that the optic tectum affords a classic example of the interrelation of structure and function. Its rise to a position of functional dominance finds its expression in a high degree of morphologic differentiation; its decline from a dominant position is associated with a decrease both in relative size and in morphologic differentiation.

EXPERIMENTS UPON THE SEGMENTATION OF SPINAL NERVES IN SALAMANDER EMBRYOS

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Communicated November 30, 1932

As a result of extirpating mesodermic somites in the embryos of Pleurodeles, Lehmann[1] was able to conclude that the typical segmentation of spinal ganglia and nerve roots occurs only when there is a normal segmental arrangement of the adjacent mesoderm, and that disturbances in the latter are accompanied by abnormal development of the former. Lehmann thus produced strong evidence to support the view that segmentation in the nervous system is not intrinsic, but is subservient to primary mesodermal metamerism. Similar experiments by the author[2] upon Amblystoma embryos have supported Lehmann's view regarding the matter of segmentation, in spite of certain differences in results regarding other phases of spinal ganglion development.[3]

In connection with experimental studies upon the growth of brachial nerves, the somites lying above the anterior limb rudiment were excised (somites 2–5) in Harrison's stages 25–27 (Fig. 1). In similar experiments

Lewis[4] showed that the limb musculature is not of somitic origin, although he did not report the effect of this operation upon limb function. The present experiments have fully corroborated the findings of Lewis, for in 86 cases with somite removal, not a single one developed without a limb (table 1).

TABLE 1

SHOWING RESULTS OF UNILATERAL EXCISION OF THE 2ND, 3RD, 4TH AND 5TH SOMITES UPON LIMB DEVELOPMENT AND FUNCTION

	WOUNDS NOT COVERED	WOUNDS COVERED
Number of operations	51	35
Died	19	0
No limb growth	0	0
Delay in limb growth	13	8
Abnormal limbs*	8	18
Normal limbs	17	16
Limbs with normal function	16	17
Limbs with restricted function	8	18
Limbs with no function	4	3

* Includes several cases with reduplications of various types.

A high percentage of limbs with normal movements (table 1) constituted functional evidence that brachial nerves are able to grow and reach the developing limb rudiment without any mechanical aid which might come through the presence of myotomes. This fact was substantiated from a study of serial sections, which showed the presence of brachial nerves in cases where axial musculature was almost or entirely absent.[5]

A study of ten cases showed that, whereas brachial nerves were present, their normal segmental arrangement and number were modified. Typically the ganglia failed to undergo normal segmentation, resulting thereby in several ganglionic masses (Figs. 2 and 3) which showed the presence of a variable number of both sensory and motor nerve roots. In many instances these could not be homologized with the roots of the opposite side.

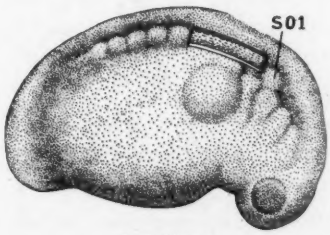

FIGURE 1

Amblystoma embryo in Harrison's stage 27+, showing excision of second, third, fourth and fifth right somites. The circular disc ventral to the denuded area indicates the position of the anterior limb rudiment. SO.1, first somite. × 10.

Although myotome absence was complete in some cases from the second to the fifth, all cases examined possessed irregularly developed neural arches on the side of operation. There is some evidence that their presence following complete somite removal is due to regeneration from the opposite

(normal) side, for in several cases where somites have been removed from both sides or where the cord has been grafted without somites, there is a complete failure of neural arches. If ganglia are capable of forming under the morphogenetic influence of cartilage, as suggested by Lehmann,[6] their irregularities in the present experiments might justly be correlated

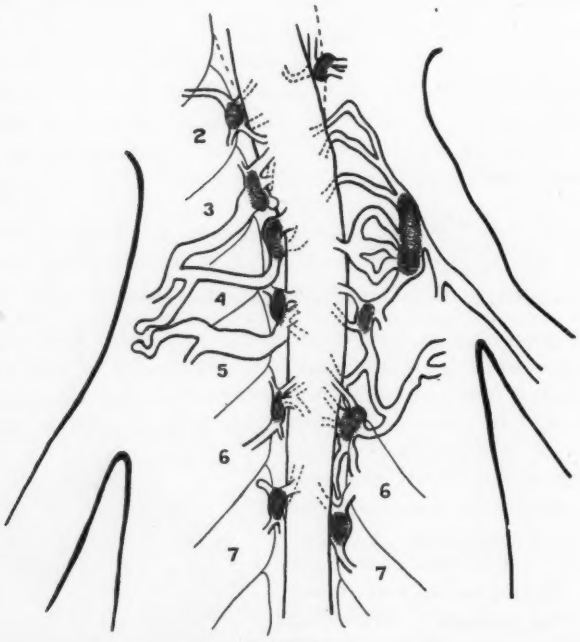

FIGURE 2

Reconstruction of spinal cord, ganglia, nerve roots and myotomes in case MEC-5 (46 days after operation). The second, third, fourth and fifth somites on the right side were removed in stage 27+. Sensory roots are in solid lines; motor roots in broken lines. Ganglia are cross hatched. × 24.

with the irregular arch formation—a matter which justifies further investigation.

The atypical arrangement of the spinal nerves in this series of experiments, the failure of complete and orderly segmentation of the ganglia, and the occasional complete loss of a spinal nerve all support the view stated above that typical segmentation of the nerves is secondary to normal mesodermal metamerism.

A second series of experiments bearing upon this problem consisted in the interpolation of one or two additional somites above the limb region.

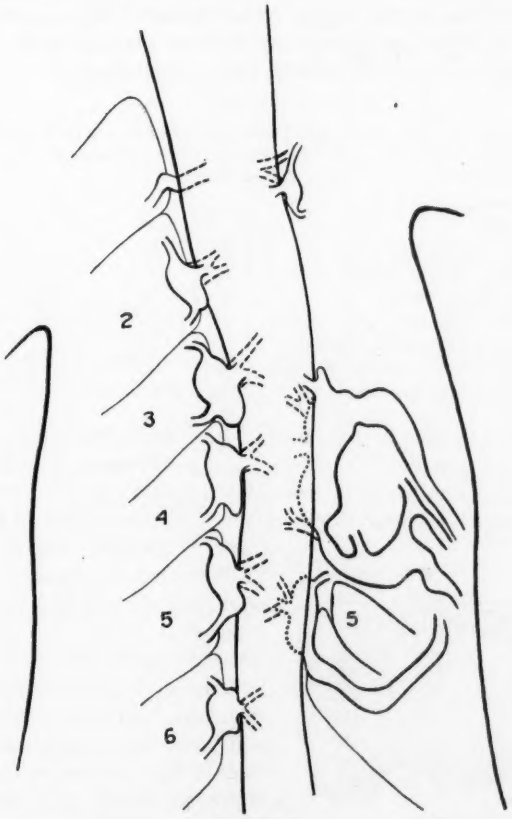

FIGURE 3

Reconstruction of spinal cord, ganglia, nerve roots and myotomes in case ME-17 (53 days after operation). The second, third, fourth and fifth somites on the right side were removed in stage 27+. Sensory roots are in solid lines; motor in broken lines. Note that the second ganglion is entirely absent, and that the third and fourth are continuous as one large ganglionic mass. × 24.

This was accomplished by removing the third, fourth and fifth somites on the right side, and grafting into the wound four or five somites from a more caudal region of another embryo (Fig. 4). This is mechanically

possible since the more caudal somites are slightly smaller in diameter. Furthermore, when they are excised as a unit, they tend to contract and can be fitted readily into a three somite wound which usually expands temporarily before healing begins. The results of this series of experiments are given in table 2, where it can be seen that in thirty-two positive cases, twenty-three developed limbs with normal function.

TABLE 2

SHOWING RESULTS OF REPLACING THE THIRD, FOURTH AND FIFTH RIGHT SOMITES BY A GRAFT CONTAINING FOUR OR FIVE SOMITES FROM A MORE CAUDAL REGION OF A DONOR EMBRYO

Number of operations	40
Deaths	8
No limb growth	0
Delay in limb growth	14
Abnormal limbs	5
Normal limbs	27
Limbs with normal function	23
Limbs with restricted function	4
Limbs with no function	5

Of ten cases studied in serial section, eight have shown the presence of a supernumerary ganglion with sensory and motor roots, as well as an additional spinal nerve, which in two cases supplied the limb. This is illustrated in figure 5. The additional nerve (*5A*) contributed to the brachial plexus. Another case of this series is illustrated in figure 6, where the additional nerve is designated as *3A*.

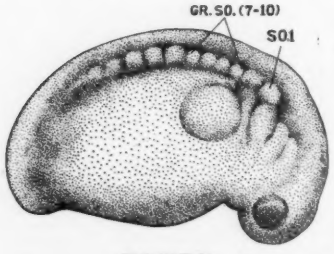

FIGURE 4

Amblystoma embryo in stage 27+, showing replacement of right third, fourth and fifth somites by the seventh, eighth, ninth and tenth from another embryo. Gr.SO.(7–10) grafted somites (7–10), SO.1, first somite. × 10.

Whereas in some instances two additional somites were grafted, no cases have been observed as yet with more than one supernumerary myotome and associated ganglion. This indicates that either one somite was destroyed during the grafting or else partial regulation has occurred. All cases thus far studied possessing a supernumerary ganglion were accompanied by an additional cartilaginous neural arch.

In a third series of experiments, an incision was made between the spinal cord and the somites. Both cord and somite surfaces were thoroughly cleaned in order that any neural crest cells which might be present could thus be eliminated. All cases examined subsequent to this operation have revealed the presence of the normal number of spinal ganglia, with

typical arrangement. These results show that either the crest cells are not yet present when the operation is done, or if they are, they regenerate

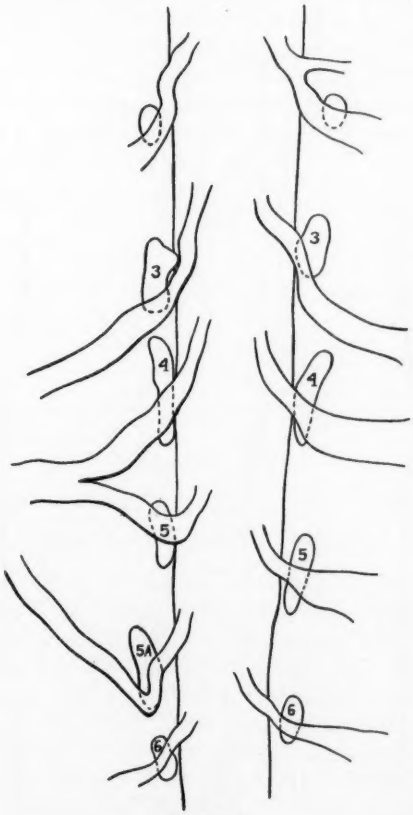

FIGURE 5

Graphic reconstruction of cord, ganglia, motor roots and peripheral nerves in case TrSO–8 (42 days after operation). The third, fourth and fifth left somites were replaced by the seventh, eighth, ninth and tenth left somites from another embryo (v. Fig. 4). Note the presence of a supernumerary ganglion and nerve designated as 5A. × 20.

and segment according to the original somite boundaries. It is thus apparent that when four somites occupy the place of three, as in the experi-

ments described above, the four ganglia which develop are determined by the somites themselves, otherwise a lack of correspondence between the

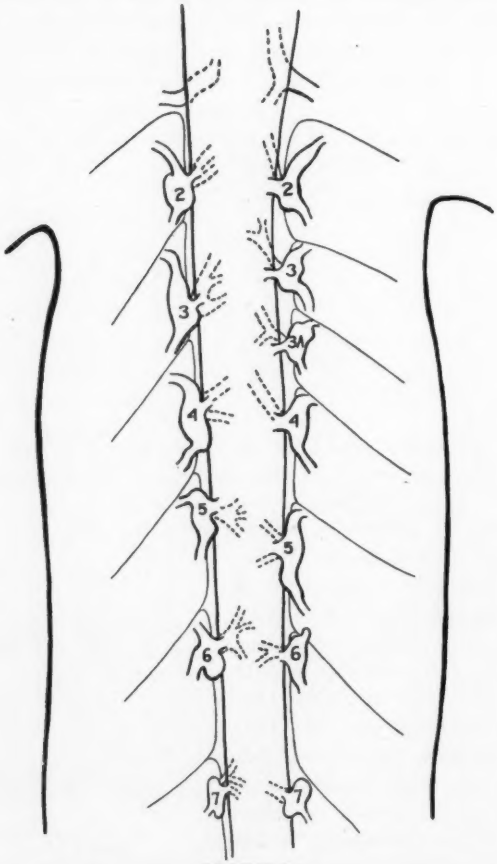

FIGURE 6

Reconstruction of spinal cord, ganglia, nerve roots and myotomes in case TrSO–37 (47 days after operation). The right limb somites (3, 4, 5) were replaced by the seventh, eighth, ninth and tenth from another embryo (v. Fig. 4). Note the presence of a supernumerary ganglion associated with the additional myotome (3A). × 24.

number of ganglia and somites would be encountered—a condition which so far has not been observed, except in the somite excision experiments

where irregular and bizarre ganglionic masses exist in the complete absence of myotomes.

The reduction in the number of ganglia and spinal nerves following somite removal, and especially an increase following the interpolation of an additional somite, constitute strong experimental support of Lehmann's view that the normal segmentation of spinal ganglia and nerves is determined by the mesodermal metamerism. There is no support of the generally held view that nervous metamerism is intrinsic, at least in the spinal cords of the forms which we have studied.

[1] Lehmann, F., *Jour. Comp. Neur.*, **49** (1927).
[2] Detwiler, S. R., *Jour. Exp. Zoöl.*, **54** (1932).
[3] Detwiler, S. R., op. cit.
[4] Lewis, W., *Anat. Rec.*, **4** (1910).
[5] The normal brachial nerves constitute the third, fourth and fifth spinal nerves.
[6] Lehmann, F., op. cit.

A CONTRIBUTION TO THE STUDY OF GALACTIC DIMENSIONS

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Read before the Academy, Monday, November 14, 1932

1. In our study of the dimensions of the galactic system, as well as in our exploration of the metagalaxy, we have been gradually driven out of the Milky Way and low galactic latitudes by increasing knowledge of the structural complexities along the Milky Way, and especially by the confusion and uncertainty caused by general and selective absorption of light near the galactic plane. Many years ago three factors had already pointed to the troubles in store for attempted analyses of galactic dimensions along the galactic circle. They were Barnard's and Wolf's work on the distribution and nature of the dark nebulae, the general consideration by many astronomers of the great rift in the Cygnus-to-Centaurus part of the Milky Way, and the recognition of the "region of avoidance," the last of special importance in showing that star clusters of any kind in low latitudes can give, when their magnitudes are appropriately corrected for light absorption, an indication of only minimum dimensions of the galaxy and the minimum distance to the center.

The region of avoidance is the mid-galactic belt, nearly ten degrees in width, in which practically no globular star clusters are found. There is another well-known region of avoidance, wider and more remote and possibly quite distinct, that affects the apparent distribution of the external galaxies in low galactic latitudes. There can be little doubt that con-

siderable numbers of clusters are behind the nearer obscuring material, mostly in Sagittarius, Scorpio and Ophiuchus.

2. I have pointed out on various occasions that certain globular clusters are partially obscured.[1] The dark nebulosity is recognizable in the vicinity of some of these affected clusters, and the stars in others seem to be abnormally faint for the angular dimensions of the systems. Presumably the light is scattered as well as obstructed and color excesses should appear, though nothing peculiar is found in the colors in Messier 22 (galactic latitude $-9°$) from an extended survey of the magnitudes of individual stars.[2]

Recently Stebbins has found, from colors determined with a photoelectric photometer and standard screens, that globular clusters in low latitude are systematically redder than those away from the galactic circle.[3] Probably this reddening is a true color excess and if so is further evidence of the light scattering in low galactic latitudes, already shown by various investigators of distant galactic clusters and Milky Way stars. It is to be noted, however, that Miss Cannon's classification of the integrated spectra of globular clusters shows later types in low latitudes. Thus we have data from Appendix A of "Star Clusters" for the following weighted means:

GALACTIC LATITUDE	NUMBER OF CLUSTERS	MEAN SPECTRUM
$> \pm 20°$	14	*F*9
$\pm 20°$ to $\pm 11°$	11	*G*3
$\pm 10°$ to $0°$	13	*G*8

The total apparent magnitudes of the low latitude clusters are on the average fainter than those in high latitude.

3. It is clear from what has been said that the globular clusters themselves can afford no conclusive evidence of the total extent of the Milky Way in the direction of the galactic circle. Still less can the galactic clusters serve in giving a value to galactic dimensions either along the Milky Way plane or at right angles to it, for they are almost wholly confined to galactic latitudes less than 10°. The examination of the whole system of observable galactic clusters, by Trumpler, Collinder, Shapley and others, accomplishes little more than the rough arrangement of those systems that are not dimmed beyond recognition by general absorption, or blocked out completely by the obscuring matter that produces the great rifts in the Milky Way and the region of avoidance. The galactic system's population of galactic clusters is probably much more incompletely known than the population of globular clusters.

Fortunately, a considerable number of globular clusters lie in the higher galactic latitudes that seem to be essentially free of light scattering and direct obscuration. They can thus give a truer picture of the over-all dimensions of the galaxy. This clearness in higher latitudes is indicated

by the essentially normal colors of extragalactic nebulae, by studies of star distribution, and by Stebbins' and my own measures of the colors of and in globular clusters.

4. Ten years ago we began at the Harvard Observatory a special survey of faint variable stars in high latitudes, in the hope of adding to information on the thickness of the Milky Way. Baade and Bailey had found faint cluster type Cepheids in high latitudes, near to, but apparently not members of, globular clusters, and their discoveries suggested that at great distances from the galactic plane there might be large numbers of these important distance-indicators. The Harvard survey was begun with plates of the MC series (16-inch Metcalf doublet). The results with this series of plates were meager, however, and some years later the systematic photometry of high latitude fields was made a part of the study of Milky Way variables. Plates of the MF series, made in Bloemfontein with the 10-inch Metcalf triplet, have proved to be of much value in the investigation.

In fourteen fields with galactic latitudes ranging from 20° to 80°, each field covering approximately one hundred square degrees, Miss Hughes has now found a large number of isolated cluster type Cepheids. Detailed data on the individual variables will be published when the study of these fields is complete. The present preliminary report is given because of the significance of the observations in galactic measurement. The results for the fourteen fields are summarized in the following table.

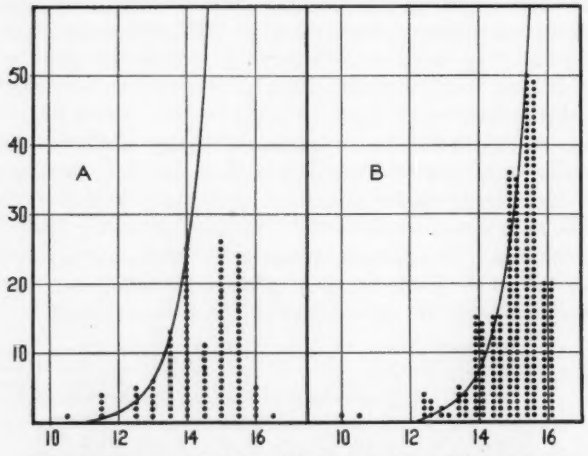
VARIABLE STARS IN HIGH GALACTIC LATITUDE

MILKY WAY FIELD	GALACTIC LATITUDE	PLATE LIMIT	NUMBER OF CLUSTER VARIABLES	FAINTEST MEDIAN MAGNITUDE	NUMBER OF NEBULAE PER SQUARE DEGREE
16	+20°	16.4	20	14.9	11
202	−20	16.6	14	15.2	0:
205	−20	16.2	6	14.2	0
204	−22	16.3	6	14.3	0
209	−39	17.0	22	15.5	10:
211	−40	16.4	13	15.8	25
212	−40	16.4	21	15.6	8
213	−57	16.4	15	15.7	15
215	−60	16.6	7	15.3	8:
216	−60	16.9	10	15.6	2:
214	−61	16.5	9	15.4	30:
6	+62	16.2	7	15.6	15
217	−80	16.7	8	15.5	20:
218	−80	16.7	9	16.1:	25

All types of variable stars are found in the high latitude fields except the classical Cepheids, but only the cluster type Cepheids are considered in the present discussion because their absolute magnitudes can be taken as a constant, and their apparent magnitudes therefore give a direct measure of distances. The limiting magnitudes given in the third column

are determined from counts of stars on the photographic plates and the van Rhijn and Seares tables relating magnitudes, star numbers and galactic coördinates. The average limit of the plates is $16^{m}.5$, and the search for cluster type variables should therefore be effective to magnitude 15.5.

Fields 204 and 205 are in the regions of the Pleiades and Orion, and the obscuring nebulosities are immediately revealed for them in the fifth column of the table, where the faintest median magnitudes of newly discovered cluster type Cepheids are 14.3 and 14.2, respectively, about a magnitude above the limit for the other fields. It is seen from this result, and from the data of the last column, that fields in galactic latitudes lower



Distribution of cluster type Cepheids in high (A) and in low (B) galactic latitudes. Coördinates are numbers of stars and mean photographic magnitudes.

than $\pm 30°$ are not sufficiently clear of obscuration for a study of galactic dimensions (except, perhaps, at certain favorable longitudes). In higher latitudes the general occurrence of extragalactic nebulae in the fields is definite evidence of a general clarity in those directions, and therefore promises greater security in exploration and measurement within the bounds of our own galaxy.

I have previously shown[4] that the irregularities in the distribution of external systems in high latitudes down to the eighteenth magnitude are to be attributed to the actual groupings of these systems, and are not to be taken as evidence of the intervention of obscuring nebulosity.

5. The discovery of numerous cluster type Cepheids fainter than the fourteenth magnitude is at once an indication of the great thickness and

extent of the galactic system, if it can be shown that these remarkable variable stars are actually members of the galactic system, and are not independent bodies in intergalactic space. The proof is both simple and direct. If the increase in number with magnitude should fall below fourfold per magnitude, as with ordinary galactic stars, a concentration to the galactic plane is indicated and we assume that the variables are members of the general galactic organization.

In figure A the number of variables for each half magnitude is shown for 121 cluster type Cepheids in the ten fields of latitude greater than 30°. The full line indicates the contour for uniform density. The marked deviation from this line shows that the cluster type Cepheids are members of the galaxy. When more fields have been examined and the survey has been taken to fainter magnitudes, it will be possible to determine the degree of concentration to the galaxy, and the actual laws of distribution.

6. As a control on the sufficiency of the MF series of plates for the survey in high latitudes, the comparable data for low latitudes are given in figure B. The material, which comprises observations of 290 variable stars in seven fields, has been compiled by Miss Swope from the data obtained for fields in the southern Milky Way, almost wholly in regions that appear essentially clear of obscuring matter. The galactic latitudes of the field centers are $\pm 75°$. Because of the great extent of the Milky Way in its plane we should not expect in these latitudes a falling off of number of variables with distance, as in high latitudes. The curve for average uniform density does, indeed, fit the observations satisfactorily. Thus it appears that the dropping off in numbers in high latitude is due to the actual thinning out of cluster type Cepheids with distance from the galactic plane.

7. The faintest median magnitudes (fifth column of the table) show that in all these high latitude fields we find members of the galactic system as much as 10,000 parsecs away. We may compute the distances in parsecs from the galactic plane and the corresponding median magnitudes from the formulae

$$d_c = \sin\beta \times 10^{0.2m_0+1}$$

$$\text{and} \quad m_c = 5 \log \sin \beta + m_0$$

where m_0 is the observed median photographic magnitude. It is readily found that if we take the absolute median magnitude of cluster type Cepheids as 0, as above, or even as $+0.5$, we have in the present survey many variables 30,000 light years from the galactic plane. A few fainter isolated cluster type Cepheids have been found at Harvard and by Baade at Bergedorf at greater distances.

The large number of variables in the present study seems to indicate that the cluster type Cepheids, as Baade has surmised, are distributed

throughout the same region as that occupied by the globular clusters; and these clusters appear more clearly than ever to outline our galaxy, as the globular clusters recently discussed by Hubble[5] and by Shapley and Mohr,[6] outline Messier 31 and the Large Magellanic Cloud. Along the galactic plane our direct measures are troubled by absorption, and we can only surmise, from the distribution of the globular clusters and cluster type Cepheids in galactic latitudes 20° to 40°, that the dimensions in this direction are much greater than shown here for the directions perpendicular to the plane.

The faintest variables in fields 209, 211 and 212 would project on to the galactic plane at a distance of more than 20,000 light years from the sun. The extension of the search to fainter magnitudes in these fields and in fields of somewhat lower latitudes will be an important step in measuring the extent of the Milky Way in its plane.

[1] E.g., in *H. Mon.*, **2**, 22 (1930).
[2] H. B. 874 (1930).
[3] Paper read at Ann Arbor meeting of the National Academy of Sciences, November, 1932.
[4] H. B. 890 (1932).
[5] *Ap. J.*, **76**, 44 (1932).
[6] H. B. 889 (1932).

THE THEORETICAL FREQUENCY DISTRIBUTION OF PHOTOGRAPHIC METEORS

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Communicated December 8, 1932

In considering the frequency distribution of meteors we must first make some simplifying assumptions before the subject can be satisfactorily treated. Let us then assume that:

1. The luminous part of the paths for all meteors is at an average height of 100 kilometers above the surface of the earth.

2. All meteors are moving with the same constant linear velocity with respect to the earth.

3. If we regard a meteor as a moving point of light, then it radiates a constant quantity of light per second.

4. If the absolute magnitude of a meteor is determined by the light radiated per unit of path when viewed perpendicular to the path at some unit distance, then there is a definite absolute magnitude distribution for meteors entering the atmosphere at the same angle.

5. All meteors from the same radiant are moving in parallel paths and are distributed with constant density over a cross-section perpendicular to the direction of motion.

Furthermore, some law of absolute magnitude distribution must be assumed. Let N_m be the number of meteors brighter than absolute magnitude m. Öpik[1] used the distribution $N_{m+1}/N_m = 4$ for meteors apparently brighter than the third magnitude. In the derivation of the curves which accompany this paper the three distributions $N_{m+1}/N_m = 3$, 4 and 5, have been used.

The apparent brightness of any meteor will depend on its distance from the point of observation, the angle its path makes with the line of sight, and the amount of atmospheric absorption present. The curvature of the earth must be taken into account; this was done by first computing frequencies on the assumption that the earth's surface is a plane and then deriving a correction for curvature which was applied to the results.

On the assumption of a plane surface the distance of the meteor will vary as sec z, where z is the zenith distance. The brightness will decrease with distance as $\sec^2 z$ but the angular velocity will decrease as sec z. We may assume that the photographic effect varies inversely as the angular velocity, and hence we have the photographic brightness decreasing as sec z owing to increase of distance from the observer. The angular velocity will also vary as sin i, where i is the angular distance from the radiant. The luminosity of the meteor therefore varies as cosec i. Absorption of the air cuts down the magnitude in proportion to the length of the air path. The photographic absorption coefficient was taken as 0.47 magnitude[2] and the length of the air path from Harvard Annals XXIII.[3] The effect of distance was combined with that of absorption and a curve drawn showing the change in apparent magnitude with zenith distance. Another curve was drawn showing the increase in magnitude with angular distance from the radiant. For a given position of the radiant, the change in apparent magnitude due to the above effects could be computed from these curves for any position in the sky. The corresponding relative numbers of meteors for the three absolute magnitude distributions were then read from curves drawn between log N_m and m

To obtain the relative frequency of meteors brighter than any given apparent magnitude another effect must be considered. As the zenith distance increases, a unit solid angle at the point of observation covers a larger area parallel to the earth's surface at any fixed height; its effect will be to increase the frequency of meteors near the horizon. This factor varies as $\sec^3 z$ and was read from a fourth curve.

There remained now to apply the correction due to the curvature of the earth. The amount of this correction was computed from a table given by Öpik.[4] Frequencies at various points were determined for single

radiants at altitudes of 15, 45 and 90 degrees. Lines of equal frequency were drawn by graphical interpolation and the resultant plots are shown in figures 1 and 2. The frequency at the radiant was found by averaging values for distances from half a degree to five degrees from the radiant. Closer than half a degree the cosec law for increase of brightness with approach to the radiant does not hold.

Figures 1 and 2 give the most probable relative frequencies over the sky for meteors belonging to a single shower. To find the values for sporadic meteors such distributions must be summed for radiants in all altitudes and azimuths. This was done, mainly by graphical interpola-

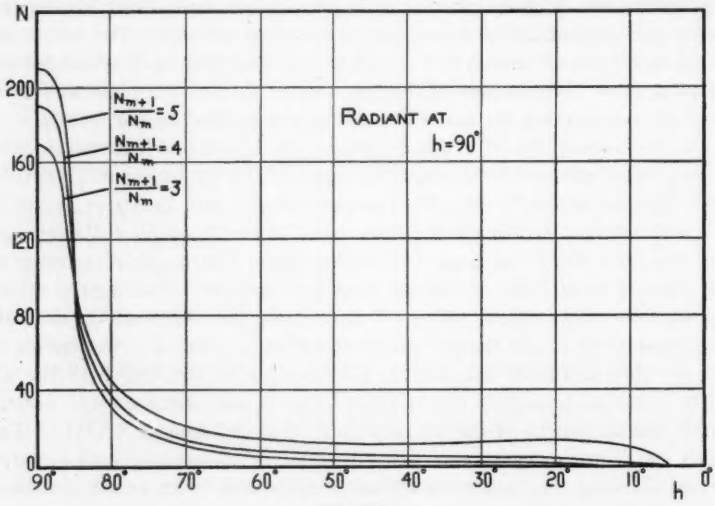

FIGURE 1

The photographic frequency of meteors with radiant at the zenith plotted against altitude h.

tion, assuming radiants distributed evenly over the whole sky. In the summation the radiants near the zenith must be given higher weight since here the meteors are coming down perpendicular to the atmospheric surface and there will be a greater number per unit area per second. For this reason meteors from the different radiants should be weighted as cos Z, where Z is the zenith distance of the radiant.

Dr. Öpik kindly placed some of his unpublished work at the disposal of the writer. According to this, which was based on both observation and theory, meteors of the same mass and velocity have luminous paths which vary in length approximately as sec Z, and hence their luminosity per unit length varies as cos Z. This variation in the length of path means

a change of magnitude of 2.5 log cos Z, and when this is translated into frequencies for the three absolute magnitude distributions used we have factors (cos Z)$^{1.20}$, (cos Z)$^{1.50}$, (cos Z)$^{1.75}$. Combining these expressions

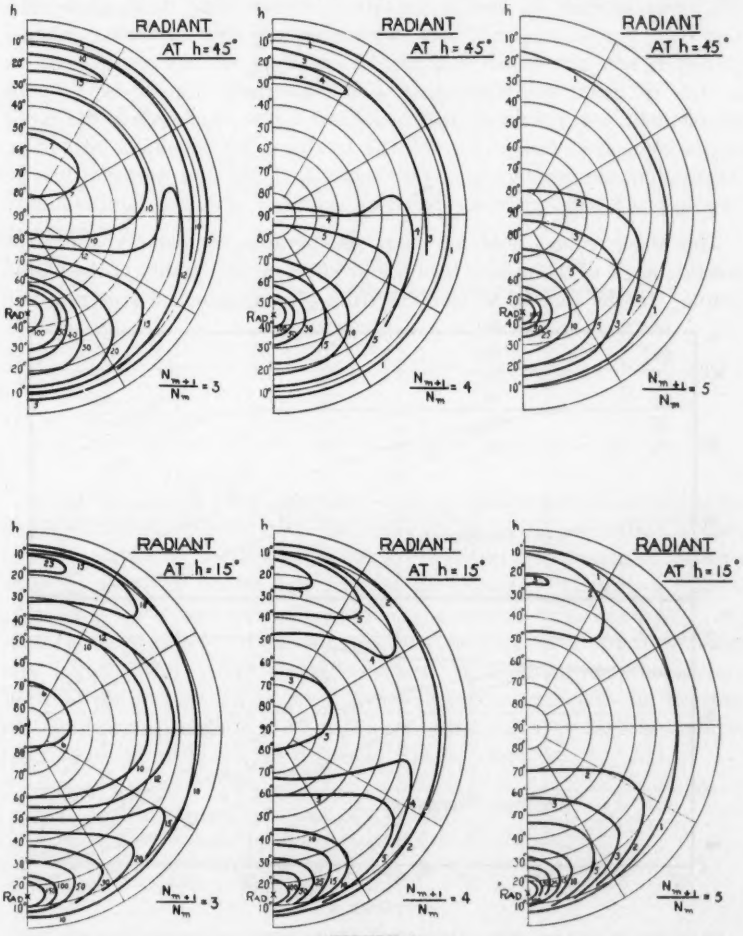

FIGURE 2

Curves showing the relative chance of photographing a meteor of any given shower in different positions in the sky. Each plot covers half of the visible hemisphere.

with the factor mentioned above we see that meteor frequencies from different radiants should be weighted as (cos Z)$^{2.20}$, (cos Z)$^{2.50}$, (cos Z)$^{2.75}$, for $N_{m+1}/N_m = 3$, 4 and 5, respectively.

The results of this summation are given in table 1 and plotted in figure 3(*a*). The relative frequencies are reduced to a scale equalling 100 at the zenith.

TABLE 1

ZENITH DISTANCE	FREQUENCY OF PHOTOGRAPHIC METEORS N_{m+1}/N_m = 3	4	5
0	100	100	100
15	100	100	98
30	100	90	86
45	98	76	56
60	96	54	28
75	80	28	8

The above values hold for chart photographs of meteors where the position angle of the meteor trail has no effect on the quality of the photograph. In the case of meteor spectrum photographs, no spectrum will

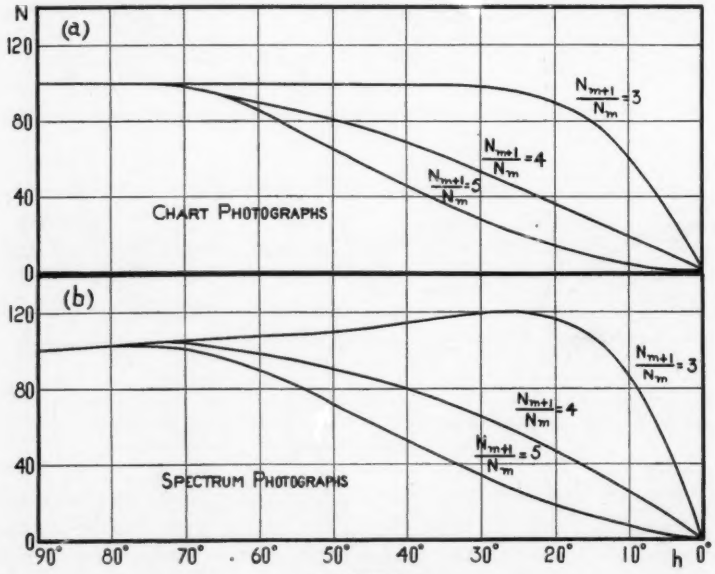

FIGURE 3

Frequency of photographic meteors for radiants distributed evenly over the sky plotted against altitude *h*.

be recorded if the meteor happens to cross the photographic field perpendicular to the refracting edge of the prism. Since there is a preferential downward motion of meteors near the horizon, while at the zenith the motions are at random, the greater zenith distances, on this

account, will have a higher weight when we are attempting to photograph meteor spectra. The amount of this effect was evaluated by dividing the sky into sections and computing the proportion of meteors coming from radiants in each section for points 15 and 45 degrees above the horizon. The effective dispersion of a spectrum photograph will vary as cos θ, where θ is the angle the meteor trail makes with the refracting edge of the prism. The weight of a photograph was taken to vary as the effective dispersion, and it was found that for meteor spectrum photography the frequency for points at altitudes of 15 and 45 degrees should be multiplied by 1.36 and 1.12, respectively, for all three absolute magnitude distributions. The resultant values are listed in table 2 and plotted in figure 3(*b*).

TABLE 2

ZENITH DISTANCE	FREQUENCY OF PHOTOGRAPHIC METEORS		
	$N_{m+1}/N_m = 3$	4	5
0	100	100	100
15	102	102	100
30	106	96	90
45	110	86	62
60	116	66	34
75	110	36	10

It will be seen that the apparent frequency distribution of photographic meteors depends greatly upon the absolute magnitude distribution used in the calculations. The assumption of a uniform distribution of radiants over the sky is of course only true on the average. There is a natural clustering of radiants near the apex of the earth's way. At 6:00 P. M., with the antapex high in the sky, the frequency at small zenith distances will fall slightly. After midnight, when the apex is near the eastern horizon, the frequencies at great zenith distances, especially in the east, will be increased slightly. At 6:00 A. M., with the apex high in the sky, frequencies at small zenith distances will be increased.

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[1] Öpik, E., *Bull. Harvard Col. Observ.* 879, 5 (1930).
[2] King, E. S., *Annals Astron. Observ. Harvard Col.*, **59**, 114 (1912).
[3] Pickering, E. C., *Ibid.*, **23**, 95 (1890).
[4] Öpik, E., *Publ. Tartu Observ.*, **25**, 7 (1922).

A SIMPLE DERIVATION OF THE DISSOCIATION FORMULA

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The formula for the ionization of a gas in thermodynamic equilibrium may be written as follows:

$$\frac{n_0'}{n_0} n_e = \frac{2(2\pi mkT)^{3/2}}{h^3} e^{-\chi_0/kT} \frac{b'(T)}{b(T)}, \quad (1)$$

where n_0', n_0 and n_e are, respectively, the number of ionized atoms, neutral atoms and electrons per unit volume. χ_0 is the ionization potential of the neutral atom. $b(T)$ is the so-called partition function of the neutral atom:

$$b(T) = g_1 + g_2 e^{-E_2/kT} + g_3 e^{-E_3/kT} + \ldots = \sum_i g_i e^{-E_i/kT}, \quad (2)$$

where the g's and E's are the weights and energies (excitation potentials) of the respective states. There is a similar "primed" expression for the ionized atom. The other constants have their usual significance.

The dissociation formula is usually obtained from either thermodynamics or statistics, but, because the derivation is long and somewhat complicated, the following simplified deduction of it may be of some value.

We start with Boltzmann's well-known formula for the distribution of atoms in different energy states:

$$\frac{n_i}{n_1} = \frac{g_i}{g_1} e^{-E_i/kT}, \quad (3)$$

where n_1 denotes the number of atoms in the lowest state of the neutral atom. The energy states of an atom consist of two kinds: discrete and continuous. On the Bohr-Sommerfeld atomic model the former is represented by electrons in elliptic orbits and the latter by electrons in hyperbolic orbits. Thus the distinction between a neutral atom and an ionized one is somewhat artificial. An ionized atom may legitimately be thought of as a neutral atom with its electron in an hyperbolic orbit. The simple Boltzmann formula, therefore, should suffice to determine the character of the ionization. The energies of the free electrons, E_i, distributed according to Maxwell's law, will be

$$E_i = \chi_0 + \tfrac{1}{2}m(v_1^2 + v_2^2 + v_3^2) = \chi_0 + \frac{1}{2m}(p_1^2 + p_2^2 + p_3^2), \quad (4)$$

where the subscripts denote the velocities (v) and the momenta (p) in the

three coördinate planes. This is merely another way of writing Einstein's equation of the photoelectric effect.

The quantum condition in its simplest form is

$$\int dp\, dq = h \quad \text{or} \quad \frac{\int dp\, dq}{h} = 1, \tag{5}$$

and, in the case of discrete orbits, it is customary to assign a quantum weight of unity to a state so defined. When degeneracy is involved, i.e., where a certain specified number (say g) of states have identical energies, it is often convenient to consider them jointly and assign to them a weight

$$g\,\frac{\int dp\, dq}{h}.$$

Where three degrees of freedom exist, this becomes:

$$g\,\frac{\int dp_1\, dp_2\, dp_3\, dq_1\, dq_2\, dq_3}{h^3}. \tag{6}$$

Now, in the region of continuous energies,[1] where quantization is not governed by (5), it is necessary, in order to keep our system of weighting consistent for the limiting cases, to adopt weights

$$g_i = g\,\frac{dp_1 \ldots . dq_3}{h^3}. \tag{7}$$

g, representing as it does the combined weights of the free electron and the ionized atom in the normal state, becomes $2g_1'$. The factor 2 arises from the two possible orientations of the electron because of its spin. Substituting (4) and (7) into (3), we obtain

$$\frac{dn_e}{n_1} = \frac{2g_1'}{h^3 g_1}\, e^{-\chi_0/kT}\, e^{-\frac{1}{2m}(p_1^2 + p_2^2 + p_3^2)/kT}\, dp_1 \ldots . dq_3. \tag{8}$$

We shall suppose that, within the volume V of at present undetermined magnitude, we shall find but one ionized atom in its lowest state, n_1 atoms still neutral in the ordinary meaning of the word and in their lowest state, and n_e electrons. Then dn_e represents the number of these electrons having momentum components in $dp_1 \ldots dp_3$ and space coördinates in $dq_1 \ldots dq_3$.

Furthermore, if dn_e is integrated with respect to the momenta and over the volume V, $\int dn_e = n_e$. Obviously, the ratio $\frac{\int dn_e}{n_1}$ may be written in the form $\frac{n_e}{n_1}$ without any restrictions as to the volume V. Thus:

$$\frac{n_e}{n_1} = \frac{2g_1'}{h^3 g_1} e^{-\chi_0/kT} \int \int_{-\infty}^{+\infty} \int e^{-\frac{1}{2m}(p_1^2 + p_2^2 + p_3^2)/kT} dp_1\, dp_2\, dp_3 \int\int\int dq_1\, dq_2\, dq_3. \quad (9)$$

$$= \frac{2(2\pi mkT)^{3/2}}{h^3} \frac{g_1'}{g_1} e^{-\chi_0/kT} V. \quad (10)$$

If there are n_1' ionized atoms in their lowest energy state, per cm.^{3} then, by definition,

$$n_1' V = 1, \quad (11)$$

which serves to determine V.

This gives:

$$\frac{n_1'}{n_1} n_e = \frac{2(2\pi mkT)^{3/2}}{h^3} \frac{g_1'}{g_1} e^{-\chi_0/kT}. \quad (12)$$

But, by the Boltzmann formula,

$$n_1 = n_0 \frac{g_1}{b(T)} \quad \text{and} \quad n_1' = n_0' \frac{g_1'}{b'(T)}, \quad (13)$$

giving, when substituted into (12), the desired equation (1).

If, instead of n_e, the electron pressure p_e (in dynes) is introduced by means of the equation of state:

$$p_e = n_e kT, \quad (14)$$

we finally get the familiar result:

$$\frac{n_0'}{n_0} p_e = \frac{2(2\pi m)^{3/2}(kT)^{5/2}}{h^3} e^{-\chi_0/kT} \frac{b'(T)}{b(T)}. \quad (15)$$

Or, taking Briggsian logarithms and introducing appropriate conversion factors,

$$\log \frac{n_0'}{n_0} = -\frac{(5040.50 \pm 0.69)I}{T} + 2.5 \log T - (6.17913 \pm 0.00056) + \log \frac{b'(T)}{b(T)} - \log P, \quad (16)$$

where I is the effective ionization potential in volts and P the electron pressure in atmospheres. The numerical values and probable errors of the constants were computed by Birge.[2]

The argument may easily be extended to cover the case of molecular dissociation. The derivation emphasizes several points that are some-

times obscured in the usual treatment. Chief of these, perhaps, is the significance of the partition function $b(T)$. The non-convergence of this function has been discussed by various writers,[3] all of whom have pointed out that the higher members of the series must be dropped because the atom hasn't the infinite room that it would require in order to develop a quantum state of indefinitely large n. The questionable part of these arguments lies in determining where the series is to be terminated. The ambiguity is partially removed by the method above. The collisions of neighboring atoms and the absorption and emission of radiation will broaden the higher atomic states until they overlap and form a continuum, say at energy χ_ϵ measured from the lowest atomic state, where the effective ionization potential, χ_ϵ, is less than the *true* ionization potential, χ_0. It is χ_ϵ, therefore, and not χ_0 that should appear in the equations, and the summation of the partition function should be taken only to $E_i = \chi_\epsilon$. W. H. Wright[4] seems to have been the first to have recognized the distinction between χ_ϵ and χ_0. The general argument he advanced to explain the appearance of continuous absorption or emission to the red of the theoretical series limit is essentially correct, although certain details based upon the Bohr atomic model cannot now be accepted.

$b(T)$ does not include, as some writers have assumed, the partition function of the free electron. When a satisfactory theory of line-broadening as a function of temperature, pressure, chemical composition, etc., has been worked out, it will be possible to calculate χ_ϵ. Doppler broadening, which arises only from relative motion of the various atoms and not from inherent "fuzziness" of the individual states, does not count. It is clear by this argument that the methods of excluded volumes as developed by Urey, Fermi and Planck will not give the correct result.

According to wave-mechanics, the half-width of a quantum state, expressed in units of frequency, is, approximately,

$$\Delta\nu_n \sim \frac{1}{4\pi T_n}, \tag{17}$$

where T_n is the mean lifetime of the atom in the state n, summed over all ways of leaving it, whether by collisional or radiational action. For hydrogenic atoms, and most atoms may be considered of this type for large values of n, the energy states are located at

$$E_n = h\nu = \chi_0\left(1 - \frac{1}{n^2}\right), \tag{18}$$

and the difference between the successive levels is

$$d\nu_n = \frac{2\chi_0}{hn^3}. \tag{19}$$

When

$$\frac{1}{2}\,dv_n \sim \Delta v_n \tag{20}$$

the levels overlap effectively to form a continuum. If $\bar{n}$ is the quantum number of the level where this occurs,

$$\chi_e = \chi_0\left(1 - \frac{1}{\bar{n}^2}\right). \tag{21}$$

For low densities, radiational transitions predominate and

$$\frac{1}{T_n} = \frac{1}{\sum_m A_{nm}}, \tag{22}$$

where A_{nm} is the Einstein coefficient of spontaneous transition to the lower state, m. Where collisions are involved, special knowledge of the type of interaction is necessary and the problem, while theoretically soluble, is very complicated. Further work on this point is in progress.

[1] See Fowler, *Statistical Mechanics*, page 17 *et seq.*

[2] *Astroph. Jour.*, in press.

[3] See discussion by Fowler, *Statistical Mechanics*, page 345 *et seq.*

[4] *Proc. Amer. Phil. Soc.*, **49**, 530 (1920); *Nature*, **109**, 810 (1922).

A SUGGESTED MECHANISM OF CLASS Be STARS

By Dean B. McLaughlin

The Observatory, University of Michigan

Read before the Academy, Monday, November 14, 1932

The Characteristic Variations of Be Spectra.—Spectrum variables of the Phi Persei type have wide emission lines of hydrogen centrally divided by absorption lines. The spectral variation consists mainly of a cyclic change of the relative intensities of the two components of each emission line. The same variations are exhibited simultaneously by all the hydrogen emission lines, although the changes are quantitatively greater for the lines of greater wave-length. A complete cycle may be regarded as a passage from the condition of equal emission components, through a stage in which the component of greater wave-length is the stronger, a second equality, thence through a stage in which the component of shorter wave-length is the stronger, followed by a return to equality. In the discussion which follows, we shall refer to the components of greater and lesser wave-length as the red and violet components, respectively.

Shifts of the emission and absorption lines are intimately connected with these changes of intensity. When the red component is more intense, the double emission and its central absorption shift toward the violet. A displacement toward the red occurs when the violet component is stronger. When the components are unequal, a strong absorption border, in some cases stronger than the central absorption, appears flanking the stronger emission component. This last phenomenon is most readily explained as due to an uncovering of a broad underlying absorption line when the emission shifts from its normal position. These changes occur in a period of 126 days in Phi Persei, but in most stars of this type the cycles are several hundred days in length.

Objections to a Binary Theory.—The cyclic variations just described may be regarded as truly periodic in Phi Persei, and they recur with considerable regularity in HD 20336.[1] It is natural to attempt an explanation in terms of binary motion. The absorption borders could easily be taken for lines of a secondary spectrum, as they occur in the positions where such lines would be expected.[2]

A binary interpretation of the large line displacements of long period would lead to unbelievably large masses for the stars. That the line displacements are not due to orbital motion is proved by the behavior of 25 Orionis,[3] which has shown cycles as long as 1800 and as short as 1200 days. A more irregular example is Pi Aquarii,[4] for which no period can now be stated. Further, binary motion gives no explanation of the changes of emission lines which are so closely correlated with the apparent variations of velocity. It is, therefore, necessary to seek an entirely different mechanism. Nevertheless, the writer proposes an interpretation in terms of a pure Doppler effect.

Emitting and Absorbing Levels in the Atmosphere of a Be Star.—In accordance with the suggestions of Rosseland,[5] Struve,[6] and others, we consider the atmosphere of a Be star to be of very great extent compared with the star itself; in effect it is to be regarded as a small planetary nebula, but the excitation is much lower than in the true planetaries, due to the lower temperature of the central star. For simplicity we shall consider the nebula to be composed of hydrogen alone. In the inner portion of this nebula the atoms would be frequently ionized by absorption of radiation from the continuous spectrum beyond the head of the Lyman series. Recombination of ionized atoms and electrons would result in the emission of the Lyman and Balmer series. Such a mechanism of the luminosity of gaseous nebulae has been proposed by Menzel[7] and Zanstra.[8]

Beyond a certain distance from the star, the atoms would be shielded from the ionizing radiation by the absorption of that light by atoms closer to the star. The outer atmosphere would thus be denied the large supply of energy required for the production of strong emission lines, and the chief

observed effect of the atoms of the outer layers is found in the absorption lines which bisect the emission.

Suggested Mechanism of Be Variation.—The very considerable width of the emission lines of many constant Be stars, and of the variables at the time of equal components, is regarded as being due to rapid rotation of the stellar atmosphere as suggested by Struve.[9] The star itself is thought of as rotating even more rapidly, so that the absorption lines produced in the reversing layer are enormously broadened. The outer atmosphere, producing the central absorption lines, is regarded as rotating more slowly than the regions of effective emission. In short, we consider the atmosphere so extensive and so rarefied that the atoms, to a first approximation, pursue independent orbits as satellites of the star.

We consider the star to be a temperature variable. In a B-type star the temperature is so high that a considerable change of temperature of the photosphere could occur without a conspicuous change of the visual or photographic brightness. To take a specific example, if the temperature changed from 15,000° to 16,000°K., the visual brightness of the star, considered as a black body, would change only 0.13 magnitude. But the same change would produce a 69 per cent increase of the radiation of wavelength 1215 Å (Lyman α). As a result, the selective radiation pressure acting on the hydrogen atoms would be increased and a general outward movement would be inaugurated.

It appears probable that the outward motion of an atom would be accelerated so long as it was within the region where radiation of wavelength 1215 Å penetrated, but in the outer atmosphere it would be screened from that radiation by the absorption produced by lower-lying atoms, hence it would be retarded by the gravitational attraction of the star. One exception, however, should be noted; in some cases the acceleration is so great that before the atom reaches the region where it is screened from the radiation, it has already attained a velocity exceeding the velocity of escape. Such a star would show a spectrum of the P Cygni type, the emission line representing the gases rushing from the star in all directions, and the absorption line displaced to the violet being produced by the gases approaching the observer on the near side of the star. Such an explanation of spectra of P Cygni and Wolf-Rayet type has been given by Beals.[10]

We now consider the resultants of the velocities of rotation and expansion and in particular the line-of-sight components of these velocities. The light from the *receding* gas on the far side of the star and at the receding limb would pass freely through the *approaching* gases in the atmosphere nearer the observer, since the Doppler effect of their relative velocities renders absorption impossible. On the other hand, light coming from the approaching gases of the inner atmosphere must pass through gases

of the outer atmosphere which are also approaching, and much of such light would be absorbed.

Thus, in figure 1, the atoms A, B and C are incapable of absorbing the light emitted by D, E and F, so that the red component of the emission

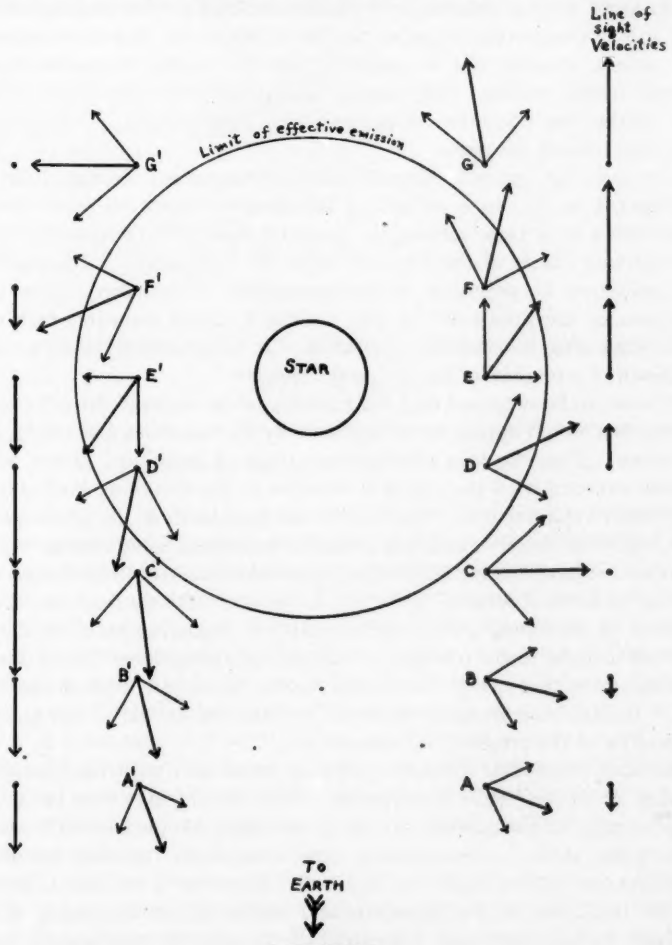

FIGURE 1

shines through brightly. The atom G would give some feeble emission, but this might be absorbed by F. The star would occult some rapidly receding gases, thereby cutting down the intensity of the extreme outer edge of the emission and having the effect of "uncovering" the broad ab-

sorption line produced in the rapidly rotating stellar reversing layer. Light from the atom G' would not be absorbed, but its emission is relatively feeble. But light emitted by D', E' and F' would suffer a large loss from absorption by atoms A', B' and C', since all have velocities of approach of the same order of magnitude. Due to small differences of these velocities and to the probable smaller number of absorbing atoms, the absorption would probably not be complete, and the violet component would remain faintly visible. The central absorption line, displaced toward the shorter wave-lengths, is produced by approaching gases between the observer and the star.

Obviously the opposite inequality (violet component stronger) may be interpreted as due to a collapsing atmosphere. Since all stars of this type which have been sufficiently observed show cyclic changes in which the extreme values of the intensity ratio are reciprocals of one another, an oscillation or pulsation of the atmosphere is indicated. The only conspicuous exceptions to this rule are the P Cygni stars in which outward streaming is occurring constantly. It is noteworthy that no case is known of a reversal of the P Cygni structure.

It is not to be supposed that the emitting layers undergo the full change of size that would appear to be indicated by the velocities and the lengths of cycles. The velocities observed are those of individual atoms which stream outward from the region of emission to the absorbing shell and are constantly replaced from below by atoms ejected from the photosphere. The region of effective emission probably undergoes some change of size, but this is regarded as being considerably smaller than the distances traveled by the individual atoms. Even so, it appears that the increase in the amount of absorbing gas as the atmosphere expands should produce a marked increase in the intensity of the central absorption. There is some evidence of such a change in the case of Phi Persei, but the fact that it is not a conspicuous phenomenon must be admitted as one of the greatest difficulties of the proposed hypothesis.

Another formidable difficulty arises in connection with the postulated change of photospheric temperature. This should give rise to a very large change in the amount of energy available for photoelectric ionization of the atoms. Consequently, large changes in the total intensities of the emission lines should be expected. However, if the star is hottest at the beginning of the expansion and coolest at the beginning of the collapse, it is evident that the extent of the emitting atmosphere would have an effect just opposite to that of the temperature, and the total intensity of the emission might remain sensibly constant.

In invoking a change of temperature as the cause of the spectral variations of Phi Persei stars, the present hypothesis makes this type of variation simply a special case of stellar variation. This is not a radical de-

parture, for some Be stars are known variables and others are suspected. The actual detection of the variations of most of these objects, however, would require many years of work with the photoelectric cell. The lack of knowledge of any variation of most of these stars cannot be admitted as evidence against the proposed hypothesis.

[1] Curtiss, *Mich. Obs. Pub.*, **4**, 167 (1932).
[2] McLaughlin, *Astrophys. J.*, **75**, 62 (1932).
[3] Curtiss, *Mich. Obs. Pub.*, **4**, 170 (1932).
[4] McLaughlin, *Ibid.*, **4**, 190 (1932).
[5] *Astrophys. J.*, **63**, 218 (1926).
[6] *Ibid.*, **73**, 96 (1931).
[7] *Pub. Astron. Soc. Pacific*, **38**, 295 (1926).
[8] *Pub. Dom. Astrophys. Obs.*, **4**, 234 (1931).
[9] *Astrophys. J.*, **73**, 100 (1931).
[10] *Pub. Dom. Astrophys. Obs.*, **4**, 294 and 297 (1930).

HOST SPECIALIZATION OF ERYSIPHE GRAMINIS TRITICI

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Marchal[4] was the first to show that the powdery mildew of grasses, *Erysiphe graminis* DC., could be separated into races, differentiated by their host specialization. He was able to distinguish seven races: *Tritici* on some of the species of Triticum, *Hordei* on a number of species of Hordeum, *Secalis* on species of Secale, *Avenae* on several species of Avena and on *Arrhenatherum elatius*, *Poae* on a number of species of Poa, and *Agropyri* on Agropyron. Salmon,[7,8] Reed,[5,6] Mains,[1] Mains and Dietz,[2] Mains and Martini[3] and Vavilov[10,11] have made extensive studies of several of these races and have shown that resistant varieties occur in a number of the susceptible species. In previous studies (Mains and Dietz[2]), it has been shown that the powdery mildew on species of Hordeum can be separated into five physiologic forms, distinguished by differences in the reaction of varieties of barley.

An investigation of the powdery mildew of wheat, *Erysiphe graminis Tritici*, has now shown that there are at least two physiologic forms in this race. These forms are sharply differentiated by the reaction of several varieties of wheat. These studies were made with seedlings inoculated in the greenhouse during the winter months. The technic of inoculation has been described in detail in previous publications,[1,2,3] giving the results of the study of other races.

Results with Physiologic Form 1.—In 1923, an extensive study of 590

varieties of wheat was made with a culture of mildew which had appeared on wheat growing in the greenhouse at Lafayette, Indiana. In 1924, 1929 and 1930 at Purdue University and in 1931 at the University of Michigan the study was continued with collections of mildew obtained from wheat from Lafayette, Indiana. During the latter years a number of additional varieties were studied and compared with the most resistant strains selected in 1923. The results cannot be given here in detail. Briefly summarized, most of the varieties of *Triticum vulgare* Vill. were susceptible. Included were strains of such varieties as China, Dawson, Democrat, Dietz, Forward, Fulcaster, Fultz, Fultzo-Mediterranean, Gladden, Gold Coin, Gypsy, Harvest King, Harvest Queen, Honor, Illini Chief, Kanred, Kawvale, Malakoff, Marquis, Meally, Mediterranean, Minhardi, Nigger, Poole, Portage, Purple Straw, Red Cross, Red Rock, Rudy, Sibley, Turkey and Velvet Chaff. A few varieties such as Axminister (C. I. 1839), Chul (C. I. 2277), Dixon (C. I. 6295), Erivan (C. I. 2397), Huron (C. I. 3315), Norka (C. I. 4377), and several selections of Illinois No. 1, specially 35, 47 and 59, were outstanding for their pronounced resistance. These, as shown in the accompanying table, exhibited little or no development of mildew through the four years of study. Norka, which was being used extensively in rust investigations, was repeatedly exposed to mildew attack and consistently exhibited a very pronounced resistance. Some varieties were variable, exhibiting very pronounced resistance sometimes while showing moderate resistance or moderate susceptibility at others. Thus, Progress (C. I. 6902) was sometimes classed as very resistant (0), at others as moderately resistant (1+). Hope (C. I. 8178) showed somewhat greater variation, usually being resistant (0–1) but occasionally approaching moderate susceptibility (2+). A selection of Michigan Amber (29–1–1–1), however, was the most outstanding in this regard. While it usually was more or less resistant (0–1), it was frequently quite susceptible (3+).

The club wheats (*Triticum compactum* Host.), were for the most part very susceptible as shown by strains of the varieties Blue Chaff, Brown Glory, Jenkins, Little Club, Mayview, Red Chaff, Termok and Washington Hybrid. Three unnamed strains were moderately resistant and one (No. 830) was very resistant in the 1929 tests.

The varieties of spelt (*Triticum Spelta* L.), were mostly susceptible. A few were moderately resistant.

The results with durum wheats (*Triticum durum* Desf.), proved to be specially interesting since most, including strains of the following varieties, Acme, Arnautka, Blanco, Buford, Goose, Hugenot, Indian Runner, Kahla, Kubanka, Mindum, Monad, Pentad and Velvet Don, were more or less susceptible. Only a few strains showed much resistance and no variety studied was outstanding for its resistance.

Only a few varieties of poulard wheats (*Triticum turgidum* L.) were studied. These were more or less susceptible, except for an unnamed strain (No. 820) which was rather resistant. The same was true for the polish wheats (*Triticum polonicum* L.), only one strain showing particular resistance.

The emmers (*Triticum dicoccum* Schrk.), on the other hand were mostly resistant, only a few strains showing pronounced susceptibility. The varieties Khapli (C. I. 4013), Vernal (C. I. 1524), White Spring (S. D. 293) and Yaroslav (C. I. 1526), showed very pronounced resistance. The few strains of einkorn (*Triticum monococcum* L.), studied were mostly very resistant. One variety, Double Einkorn, was moderately resistant. Likewise, the few strains of *Triticum dicoccoides*, *T. persicum*, and *T. timophevii*, studied showed pronounced resistance. Several strains of *Triticum stramineum* were moderately susceptible, while others were very resistant.

All the wild grasses studied proved to be very resistant. The following species were inoculated: *Agrostis alba* L., *A. perennans* (Walt.) Tuckerm., *Agropyron cristatum* J. Gaert., *A. repens*(L.) Beauv., *Arrhenatherum elatius* (L.) Beauv., *Bromus ciliatus* L., *B. erectus* Huds., *B. hordeaceus* L., *B. japonicus* Thunb., *B. mollis* L., *B. pumpellianus* Schibn., *B. secalinus* L., *B. tectorum* L., *Festuca elatior* L., *F. rubra* L., *Elymus canadensis* L., *E. condensatus* Presl., *E. striatus* Willd., *E. virginicus* L., *Hordeum jubatum* L., *H. murinum* L., *H. nodosum* L., *H. pusillum* Nutt., *Hystrix Hystrix* Millsp., *Secale montanum* Guss. and *Sitanion Hystrix* (Nutt.) J. C. Smith.

Physiologic Form 2.—During the winter of 1932 a culture of mildew from the vicinity of Ann Arbor was studied in the greenhouses of the University of Michigan. As shown by the accompanying table this culture is distinguished very sharply by the reaction of Axminister and Norka which were very susceptible (4) to the Ann Arbor culture. Both of these varieties had previously been highly resistant (0) to the cultures from Indiana. The race *Tritici* can, therefore, be separated into two physiologic forms by the reaction of these varieties.

This physiologic form has not been studied on such an extensive series of varieties as was used for physiologic form 1. Over 300 wheats, belonging mostly to *Triticum vulgare*, but also including a number in each of the other species studied for p.f. 1, were inoculated with p.f. 2. In most cases the reactions were similar to those found for p.f. 1. No case was noted where a variety susceptible to p.f. 1 was resistant to p.f. 2. A number of varieties were resistant to both physiologic forms. Data for several of these are given in the accompanying table.

A number of species of Aegilops were inoculated with p.f. 2. All proved to be more or less resistant. *Aegilops squarrosa* L. and *A. ventricosa* Tausch. were moderately resistant while *A. crassa* Boiss., *A. cylindrica*

Host., *A. ovata* L. and *A. triuncialis* L., were very resistant. A number of strains of rye, *Secale cereale* and *Secale montanum* showed no signs of infection when inoculated.

Therefore, as far as studied in this investigation, *Triticum vulgare*, *T. compactum*, *T. Spelta*, *T. durum* and *T. turgidum*, were mostly susceptible in the seedling stage to the *Tritici* race of *Erysiphe graminis*. However, more or less resistant varieties occurred in all of these. The varieties Chul (C. I. 2227), Dixon (C. I. 6295), Huron (C. I. 3315), Red Fern, Sonora (C. I. 4293) and Illinois No. 1 selections 35, 47 and 59 were outstanding for pronounced resistance throughout the study to both of the

TABLE 1

REACTION OF WHEAT VARIETIES TO PHYSIOLOGIC FORMS OF *Erysiphe graminis Tritici**

VARIETY	ACCESSION NUMBER	PHYSIOLOGIC FORM 1 1923	1924	1929	1930	1931	PHYSIOLOGIC FORM 2 1932
Axminister	C.I. 1839			0	0	0	4
Chul	C.I. 2227	0	0	0	0	0	0
Dixon	C.I. 6295				0	0	0–1
Huron	C.I. 3315	0	0	1–	0–1	0	0
Illinois No. 1	Sel. 35				0–1	0	0
Illinois No. 1	Sel. 47				0–1	0	0
Illinois No. 1	Sel. 59				0	0	0
Malakoff	C.I. 4898	4	4	4	4	4	4
Norka	C.I. 4377	0	0	0	0	0	4
Red Fern		0	0	0	0	0	0
Sonora	C.I. 4293	0	1	1–2	0–1		0
Mindum	C.I. 5296	3		4	4		3–4
Monad	C.I. 3320	3			4		4
Vernal	C.I. 1524	0	0	0	0–1	0	0
Khapli	C.I. 4013	0	0	0	0	0	0
White Spring	S.D. 293	0	0	0	0	0	0
Einkorn	C.I. 2433	0		0	0		0
Double einkorn		1–2		2–3	2+		2

* 0 highly resistant, little or no signs of infection.
1 very resistant.
2 moderately resistant.
3 moderately susceptible.
4 very susceptible.

physiologic forms of the mildew. Several varieties, notably Norka (C. I. 4377) and Axminister (C. I. 1839) differ markedly in their reaction to two physiologic forms of the mildew which they serve to differentiate. *Triticum dicoccum*, *T. monococcum*, *T. dicoccoides*, *T. persicum*, *T. timophevii* were for the most part resistant. A few varieties of *T. dicoccum* were more or less susceptible. The species studied of Aegilops, Agrostis, Agropyron, Bromus, Festuca, Elymus, Hordeum, Hystrix, Secale and Sitanion were mostly highly resistant.

* Part of this study was made while the writer was a member of the Department of Botany, Purdue Agricultural Experiment Station and of the Office of Cereal Crops and

Diseases of the United States Department of Agriculture. It has been continued at the University of Michigan. Paper of the Department of Botany and of the University Herbarium, University of Michigan No. 397.

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*REGENERATION IN MUTILATED SEEDLINGS**

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Van Tieghem[9] in his studies on Helianthus and Mirabilis found that cotyledons and isolated hypocotyls could be induced to root and that new plants could be grown from them. Blociszewski[1] found that isolated cotyledons of Pisum and Lupinus developed roots. Zabel[10] made similar observations concerning Pisum and Borrago. Küster[6] carried out studies on regeneration in several species of the Cucurbitaceae, and Kanzler[4] observed rooting of cotyledons in a single species, *Galium aparine*. More recently Kowalewska[5] has experimented with Pisum and Phaseolus, and Fuja[3] has studied root and shoot regeneration from cotyledons of *Cucurbita pepo*, *Cucumis sativus* and *Lupinus albus*. The writer discovered regeneration of roots and buds in *Phaseolus vulgaris* by accident, and thereby became interested in determining whether the small number of species in which regeneration was known to occur could not be increased. The

present paper is a result of that interest. Some attention was given to both Monocotyledonea and Dicotyledoneae, but only the latter group is considered in this paper.

Method.—Seeds were sterilized with calcium hypochlorite according to the method described by Wilson.[8] They were then laid on moist filter paper in sterile petri dishes and allowed to germinate there. The length of time of exposure to the sterilizing solution was varied according to the resistance of the seeds to the solution, and the degree of difficulty of sterilization of each type of seed. In some cases numerous trials had to be made, but in practically all cases it was possible to secure sterile seedlings.

When the seedlings were well out of the seed coats they were mutilated in various ways with a sterile knife, and again placed on moist filter paper in sterile petri dishes to allow regeneration to take place.

In some cases agar made with Shive's nutrient solution[7] and 2% agar-agar was used in place of the wet filter paper. In other trials 1% of dextrose was added to the Shive's nutrient agar. Numerous cultures became contaminated with fungi but, except in cultures on the agar containing sugar, bacteria did not cause any difficulty. By exercising care cultures of nearly all species were kept sterile for a period long enough to test their regenerative powers.

All these tests were performed at room temperature in the laboratory. Trials were made in both light and darkness for many of the species, but some species were tested only in light.

TABLE 1

REGENERATION OF MUTILATED SEEDLINGS ON MOIST FILTER PAPER IN PETRI DISHES

FAMILY	SPECIES	NUMBER OF DAYS REQUIRED TO DEVELOP ROOTS ON ISOLATED COTYLEDONS	NUMBER OF DAYS REQUIRED TO DEVELOP SHOOTS ON ISOLATED COTYLEDONS	NUMBER OF DAYS REQUIRED TO DEVELOP ROOTS ON BASES OF CUT HYPOCOTYLS
Urticaceae	*Cannabis sativa*	23	..	8
Polygonaceae	*Fagopyrum esculentum*	7	..	4
Caryophyllaceae	*Silene vulgaris*	11	..	16
Calycanthaceae	*Calycanthus florida*	20	40	21
Cruciferae	*Rhaphanus sativus* (radish)	9	..	4
Cruciferae	*Brassica oleracea* var. *capitata* (cabbage)	7	25	4
Cruciferae	*Brassica caulorapa* (kohlrabi)	14	58	14
Cruciferae	*Brassica pekinensis* (celery cabbage)	23	..	16
Cruciferae	*Brassica napus* (rape)	12	..	19
Cruciferae	*Brassica alba* (white mustard)	16	..	14
Cruciferae	*Alyssum saxatile* var. *compactum*	28	..	..
Cruciferae	*Brassica rapa* (turnip)	14	..	..
Cruciferae	*Brassica oleracea* var. *gemmifera* (Brussels sprouts)	12	..	7

TABLE 1 (*Continued*)

Rosaceae	*Agrimonia eupatoria*	10	..	None
Leguminoseae	*Pisum sativum*	16	15	15
Leguminoseae	*Lathyrus latifolius*	37	..	None
Leguminoseae	*Lupinus albus*	17	18	23
Leguminoseae	*Vicia faba*	9	7	7
Leguminoseae	*Phaseolus vulgaris*	10	16	8
Leguminoseae	*Gleditsia triacanthos*	30	..	None
Leguminoseae	*Thermopsis caroliniana*	29	..	29
Leguminoseae	*Robinia pseudo-acacia*	15	15	None
Leguminoseae	*Medicago sativa*	None	22	7
Tropaeolaceae	*Tropaeolium majus*	28	..	5
Linaceae	*Linum usitatissimum*	4	22	4
Linaceae	*Linum perenne*	6	25	6
Simarubaceae	*Ailanthus glandulosa*	29	6	..
Euphorbiaceae	*Ricinus communis*	..	..	15
Aceraceae	*Acer negundo*	35	41	..
Balsaminaceae	*Impatiens balsamina*	9	10	4
Malvaceae	*Hibiscus esculentus*	..	21	7
Malvaceae	*Althea rosea*	14	..	None
Umbelliferae	*Daucus carota* var. *sativa*	20	..	10
Boraginaceae	*Cynoglossum chinense*	7	..	5
Solanaceae	*Lycopersicon esculentum*	7	12	4
Solanaceae	*Capsicum frutescens* var. *grossum*	..	..	43
Cucurbitaceae	*Cucurbita pepo*	9	17	9
Cucurbitaceae	*Cucurbita maxima*	17	20	12
Cucurbitaceae	*Citrullus vulgaris*	21	21	4
Cucurbitaceae	*Cucumis sativus*	10	..	None
Cucurbitaceae	*Cucumis melo*	12	20	22
Compositeae	*Helianthus annuus*	8	17	9
Compositeae	*Heliopsis pitcherianum*	8	..	8
Compositeae	*Lactuca sativa*	17	..	10
Compositeae	*Arctium lappa*	29	18	13

Regeneration of Cotyledons.—The cotyledons were cut off with care to make sure that none of the hypocotyls were included, and an attempt was made to avoid including any axillary buds. Table 1 lists the species which formed roots and gives the rate of regeneration.

In plants with petioled cotyledons some of the cotyledons were tested with petioles intact, others with the petioles excised. The bases of the laminae rooted as readily and rapidly as the bases of the petioles.

The majority of the cotyledons with petioles produced roots at the bases of the petioles. Usually the roots emerged from the vascular bundles in the cut end of the petiole, and as a general rule, they appeared without the preliminary development of callus. In the tomato, and in the cabbage a small callus sometimes preceded the appearance of roots. In members of the Cucurbitaceae a small callus almost always developed before the roots.

Some anomalies in the position of roots on cotyledons have appeared. Pumpkin cotyledons have developed roots from the middle of the lamina, both along the midrib and away from the midrib. These roots arose from small masses of callus, and appeared to have been the result of wounds. The tomato has also produced roots from the midrib above the base of the cotyledon. The garden balsam retains its cotyledons for a long time, both on normal seedlings and on those from which the plumules have been removed. When these older cotyledons are allowed to regenerate they do not develop roots at the cut end of the petiole, but at varying distances above the base. The roots emerge from the upper, or the lower surface of the petiole depending on which is in contact with the wet paper. Frequently roots are produced from the midrib half-way up the blade of the cotyledon.

In the radish, and in buckwheat, roots have been formed on petioles or on midribs of cotyledons which had not been detached from their hypocotyls. Such cotyledons lay in contact with the moist surface of the filter paper, and it appeared that the roots had resulted from small wounds.

The time required for rooting of cotyledons ranged from four days in flax to 35 days in box-elder. Neither size of seed nor systematic position of the species appear to have any considerable influence on the rate of regeneration. Tomato, radish, buckwheat, sunflower, Brussels sprouts, garden balsam and pumpkin cotyledons all root quickly, though they vary greatly in size and family relation.

The age of the seedling when the cotyledons are detached appears to have some influence on the rapidity of regeneration as has been noted by Fuja.[3] But this influence is of less importance in some species than in others, depending on the rate at which the reserve food in the cotyledons is exhausted. In two species, *Helianthus annuus* and *Alyssum saxatile*, cotyledons from unripe seeds produced roots, though not more rapidly than those from ripe seeds.

Seedlings of tomato, garden balsam, kohlrabi and pumpkin were grown in soil for 58 days, then cut off and put in dishes on wet paper. The seedlings of another set of each of these species had the plumules cut out as soon as they began to grow. These seedlings were grown for 58 days also, when the cotyledons were considerably larger than those on the normal plants. These cotyledons were cut off also and placed on moist paper in petri dishes. Roots were formed by all the cotyledons, both from normal and from decapitated plants. The kohlrabi cotyledons rooted in 7 days, whereas cotyledons from freshly germinated seedlings of this species required 14 days to root. The old cotyledons of balsam rooted in 10 days, while those from young seedlings needed 9 days. Cotyledons from young tomato seedlings rooted in 7 days, while the 58-day cotyledons required 11 days for the process. Young pumpkin cotyledons rooted in 9 days, and the 58-day cotyledons did not form any roots until 14 days had elapsed.

None of these cotyledons had lost their regenerative capacity, and in two species it appeared to have been increased. The cotyledons on the decapitated seedlings were unable to use their food supplies in continued growth of the seedling, since all new buds had been cut off as rapidly as they appeared, and it was anticipated that they would be able to regenerate. However the cotyledons on the normal seedlings had an opportunity to pass their reserve food into the growing plants, and the fact that they still had sufficient food resources to form roots when detached, indicates that, in some species at least, the growing seedling does not draw on the cotyledons as heavily as it has been thought to do. In the common bean the food is withdrawn from the cotyledons very rapidly, and these organs soon wither and fall. In one case a cotyledon was noted which apparently had suffered an injury to its petiole which prevented the removal of food. It remained plump, and green, long after the normal cotyledons had fallen. The wide variability in the behavior of different plants makes it unsafe to generalize concerning the rate of diminution of regenerative capacity.

Regeneration of Segments of Cotyledons.—In addition to the preceding studies on whole cotyledons tests were made of the regeneration of portions of cotyledons. Cuts were made crosswise of cotyledons dividing them into apical and basal portions, and lengthwise of other cotyledons dividing them into right and left halves. Still other cotyledons were divided into smaller segments.

Basal halves of cotyledons root in quite the same way as whole cotyledons in most of the species tested. They differ only in having a smaller food supply, and ordinarily one would expect them to have food enough to enable them to root. The apical halves of cotyledons usually produce a pad of callus at the cut end of each of the main veins. These upper halves of cotyledons have produced roots in flax, Chinese cynoglossum, Brussels sprouts, tomato, sunflower, pumpkin, squash, celery cabbage, garden balsam and buckwheat. The period required for rooting these parts of cotyledons is from two to four times as long as for whole cotyledons. In some species roots are produced from the midrib only, but in others they are developed from the other principal veins as well, so that a row of roots extends across the cut surface.

Right and left halves of cotyledons cut lengthwise have produced roots in sixteen species. The roots developed at the basal tip of tissue. When cotyledons are halved in a diagonal direction roots are formed at the cut ends of the basal veins on each segment.

Small segments of cotyledons have formed roots in pumpkin, squash, buckwheat and tomato. In each of these a small mass of callus developed at the basal part of the fragment and from this a root appeared. The smallest part of cotyledon found capable of rooting was 3 mm. square. Pieces of tomato and squash cotyledons of this size produced roots.

The Effect of Light.—Neither light nor darkness appears to be capable of inhibiting root formation on cotyledons. Most species regenerated in either light or darkness, and appeared rather indifferent as regaded the influence of light. Tomato, watermelon, white mustard, flax, kohlrabi, Brussels sprouts, turnip, sunflower and pumpkin cotyledons rooted slightly sooner in light than in darkness, while radish cotyledons regenerated more rapidly in darkness. Once the roots had appeared, they developed more rapidly in the dark in almost all species. This was especially noticeable in the tomato.

The Effect of Nutrient Solutions.—Cotyledons of cabbage, white mustard, radish and garden balsam were tested on agar made by adding 2% of agar-agar to Shive's nutrient solution, and on agar made by adding 2% of agar-agar and 1% of dextrose to Shive's solution. On Shive's agar without sugar, radish and white mustard cotyledons rooted in 6 days. Balsam cotyledons rooted in 7 days and those of cabbage in 10 days. By comparison with table 1 it may be seen that, with the exception of the cabbage, the rate of regeneration has been increased greatly.

On Shive's agar with dextrose, radish cotyledons produced roots in 6 days; balsam in 17 days; cabbage in 19 days; and mustard in 20 days. The cultures of the last two species became contaminated with bacteria and fungi. It is possible that bacteria may have been present on the cotyledons of balsam though they were not apparent. Since no advantage appeared to result from the use of sugar in the nutrient solutions, and none was to be expected where the cotyledons were stored with food, no further steps were taken in this direction.

Growth of Cotyledons on Soil.—After they had become well rooted cotyledons of flax, pumpkin, watermelon, lettuce, cabbage, muskmelon, tomato, garden balsam, burdock, box-elder, kohlrabi, black locust, lupine, Chinese cynoglossum, horse bean and sunflower were planted in pots of earth. All of these grew but a number were destroyed by rats two or three weeks after they were planted. A number of others increased in size until they were twice the size of normal cotyledons on seedlings. In this enlarged form they were capable, apparently, of making their own food, for they were bright green. They formed plants without any means of extending their growth, but, otherwise able to lead an independent existence. Rooted cotyledons of several species lived for six months when they were abandoned. Others had lived nearly as long but had finally succumbed to attacks of thrips, sow bugs, etc., to which they were subject from time to time.

Development of Shoots on Cotyledons.—Some of the rooted cotyledons formed buds after a time as is indicated in table 1. Not all the cotyledons of a species formed buds, but some remained in the vegetative condition described in the preceding paragraph. Some other species produced shoots on the cotyledons while still in the petri dishes. In some

cases, okra for example, the cotyledons could not be planted in soil, for although shoots were formed, no roots were developed.

Whether the shoots were produced on cotyledons in the soil, or in culture dishes, they developed normally. In some cases they developed into plants, which ultimately became normal, though somewhat unusual in appearance at first. Species in which cotyledonary shoots were grown to considerable size are: *Acer negundo, Cucurbita pepo, Cucurbita maxima, Phaseolus vulgaris, Vicia faba, Lupinus albus, Brassica oleracea* var. *capitata, Lycopersicon esculentum, Linum usitatissimum* and *Pisum sativum*. Although not all the species noted in table 1 as having formed buds were carried through further stages in the development of those buds, there appears to be no reason why they could not have been grown to maturity from those shoots. An exception must be made of those forms which did not develop roots on the cotyledons, or on the shoots. The okra did not form any roots in the course of these experiments, and the pea usually failed to produce them on the cotyledons, but developed an adequate number at the base of the shoot just above the cotyledon.

The question of the origin of the buds on these cotyledons has not been answered as yet. If buds were present on the petioles they must have been somewhat removed from the axils for the petioles were cut off at a little distance from the hypocotyls. In one instance a bud arose on a petiole of a cabbage cotyledon about half-way between the base of the petiole and the blade, and a bud developed from a pad of callus almost midway between the base and the top of a cotyledon of box-elder. External examination has failed to show the presence of buds on the bases of any of the cotyledons observed in these studies. Fuja[3] has found that shoots on cotyledons of *Cucurbita pepo, Lupinus albus* and *Lupinus luteus* are developed from buds already formed when the cotyledons were cut off, and suggests that other cases of shoot regeneration are due also to the presence of pre-formed buds. She has observed a few cases in which buds were developed from callus on *Cucurbita pepo, Cucumis sativus* and *Lupinus albus*, and Kowalewska[5] has observed a similar origin of shoots in Phaseolus and Pisum. If all the species listed for shoot production in table 1 have pre-formed buds on their cotyledons, that condition must be much more common than has been suspected.

The following species have failed to develop roots on their cotyledons: *Beta vulgaris* (blood beet), *Beta vulgaris* var. *cicla*, (Swiss chard) *Aquilegia dichroa, Aquilegia hispanica, Aquilegia formosa, Geum urbanum, Geum tyroliensis, Colutea arborescens Albizzia julibrissin, Baptisia leucantha, Astrafalus cicer, Rhus glabra, Acer saccharum, Abutilon indicum, Solanum melongena* var. *esculentum, Pentstemon grandiflora* and *Prenanthes sp.* Possibly some of these might produce roots on further trial, for most of the cotyledons remained alive for long periods. However, two of the mem-

bers of the Chenopodiacea, the blood beet and Swiss chard, were tried repeatedly and it appears that members of that family lack the ability to regenerate either from cotyledons, or from cut hypocotyls. The egg-plant, *Solanum melongena* var. *esculenta*, was tested several times also, and contrasts strikingly with the behavior of the tomato. The pepper, *Capsicum frutescens* var. *grossum*, failed to develop roots on cotyledons though the hypocotyls rooted. Several other species are shown in table 1, in which the cotyledons did not root though the hypocotyls did. In the okra, *Hibiscus esculentus*, the cotyledons developed shoots but did not root.

Regeneration of Hypocotyls.—Hypocotyls severed immediately above collet.—After the seedlings had emerged from their seed coats the hypocotyls were severed at their bases just above the collet, or root collar. They are then placed on moist paper in the manner already described.

Table 1 shows the length of time required for regeneration of roots at the bases of the hypocotyls in the species in which it occurred. It should be noted that only those marked as failures in table 1 are known not to have rooted under the conditions of the experiment. The blanks indicate that no trial was made of the species concerned.

In almost all species the rooting is prompt and effective, so that the seedling resumes its growth with little interruption. In some species the rooted hypocotyls were planted in soil where they grew into normal plants. Most of the others appeared capable of growth to maturity, though a few were weak, and not well supplied with roots.

A comparison was made of hypocotyls cut just above the collet, and others severed near the cotyledons leaving only a short piece of hypocotyl intact. The short pieces of hypocotyl rooted as well as the longer ones, but the time required was usually twice as long as that needed by full length hypocotyls.

Effect of Various Cultural Conditions.—In general the hypocotyls will root in light, or in the dark, but certain preferences are shown, balsam and radish hypocotyls are alike in requiring four days' time for the appearance of the first root but while the radish shows more roots and larger ones in the dark than in light, the balsam acts in a directly opposite manner. The tomato is indifferent as to light affect, though the roots grow faster in the dark once they are initiated. Watermelon hypocotyls root in the dark in half the time which they require in light, while the cabbage roots in the dark in one-fifth the time which it needs for the process in light. Even after 20 days' time the roots are so few and so small that one can scarcely say that it really roots at all in light. White mustard roots rather feebly in light and not at all in the dark.

The use of agar made with Shive's solution, in place of filter paper wet with distilled water, increased the rate of root formation on hypocotyls to a remarkable extent. Cabbage, radish and garden balsam hypocotyls

rooted in three days on this substance, although they all required four days to root on filter paper wet with distilled water. Mustard hypocotyls were slow to root on wet paper, 14 days being needed for the process, but on Shive's agar they formed roots in 5 days.

Shive's agar with dextrose did not prove so good a medium for rooting as the same agar without sugar. Cabbage, garden balsam and radish all required 5 days to root on this medium, one day more than they needed on the filter paper. The sugar is certainly of no advantage, and makes the matter of keeping the cultures free of contamination a difficult one. It seems likely that contamination by unseen bacterial colonies was the explanation of the slowing effect of the sugar agar.

Position and Polarity of Roots on Hypocotyls.—The hypocotyls of all species appeared to produce roots all round, without regard to whether they appear on upper or lower sides of the stem. After the roots have emerged from the hypocotyls for a little distance they become normal in their geotropic response, and those which started upward from the stem, turn and grow downward. On some hypocotyls roots seemed to emerge from any point of their circumference, but on others the roots were formed at wide intervals, doubtless in connection with the arrangement of the vascular bundles in the steles.

Hypocotyls Severed Immediately Above Collet and Immediately Below Cotyledons.—Hypocotyls without cotyledons or roots are rigorously limited in their food stores, and it is not to be expected that many will be able to develop new roots, or buds, in the short time which is needed to bring them to the point of starvation. Perhaps the habit of storing much, or little, food temporarily in the hypocotyl may determine whether the structure produces new roots and shoots, or does not. By far the larger number of hypocotyls linger for a time and then perish without regenerating. Roots were developed on such hypocotyls in tomato, carrot, lettuce and lupine, while new buds appeared on tomato, carrot, pumpkin and watermelon.

Hypocotyls Severed Immediately Below Cotyledons but with Roots Left Intact.—Seedlings mutilated in this fashion are in somewhat less straitened circumstances than those in the preceding category, since the root system is not disturbed. However, the species which produced shoots are the same as in the preceding group. Flax was not tried, but Burns and Hedden[2] found that flax seedlings with roots in soil, and hypocotyls in a moist atmosphere were able to produce buds. Up to the present time relatively few species have been found to have the ability to form new buds under the conditions of the experiment of Burns and Hedden, and it is not surprising that so few were found to regenerate in the present trials.

Experiments with Excised Roots.—Excised roots of a number of species were kept on moist filter paper, and some of them remained alive for a month or more. At first they continued growth at the tip, but this growth

became less and less, until it finally ceased, after which the roots began to die at the upper ends and finally collapsed completely. Trials were made also with whole root systems of seedlings which had been cut away from the hypocotyls just above the collet. The short stub of hypocotyl proved unable to form buds, and usually perished before the roots. These root masses usually lived longer than excised individual roots, but were equally powerless to form buds.

Seedlings with Excised Cotyledons.—It would appear likely that seedlings from which the cotyledons had been removed leaving the plumules intact, would be able to continue growth from these plumules. However, such seems not to be the result when such seedlings are placed on wet filter paper in moist chambers. Several species were used, but in all of them the plumules failed to unfold, and death resulted without any change having taken place, except a limited amount of growth at the root tips, and a slight extension of the hypocotyls.

Discussion.—Blociszewski[1] found that detached cotyledons produced roots in peas and lupines, but reported that only the parts which had been attached to the embryonic plant was able to form roots. Fuja[3] failed to secure roots on the upper halves of lupine cotyledons sliced transversally, but did secure rooting of upper halves in *Cucurbita pepo*. In one case Kowalewska[5] rooted an upper half of a cotyledon of *Phaseolus vulgaris*. Beside *Cucurbita pepo*, the present investigation showed that nine other species were capable of such regeneration.

The rooting of severed hypocotyls seems to have been given little attention. Van Tieghem[9] reports that plumules were capable of developing into new plants in *Helianthus annuus*, and here the new roots must have been formed on a portion of the hypocotyl. In this paper it is shown that the hypocotyls of most species develop new roots in a short time, although a few species failed entirely in this respect.

So far as the rooting of cotyledons is concerned the results of the present study are in substantial agreement with Van Tieghem, Küster, Kowalewska and Fuja. However, they have greatly increased the number of species in which this type of regeneration is known to occur and have added to the knowledge of the conditions most favorable to it.

Now that it is known that cotyledonary regeneration is possible in many species, and a number of families, it becomes important to determine the internal conditions leading to such regeneration. This will be a difficult end to reach, but a step toward it will be the discovery, for comparison, of species, genera and perhaps families in which regeneration is impossible. The beet and Swiss chard have failed so completely to produce roots on either cotyledons or hypocotyls, that it appears that we have in them, two varieties of a species without any capacity for regeneration. If, indeed, they are surely incapable of developing any new growths, a

comparison of them, with regenerating species, may give some clue to the fundamental causes of all regeneration in plants.

Summary.—1. Regeneration of mutilated seedlings was tested on moist filter paper in petri dishes, and on agar made with Shive's solution. Regeneration took place more rapidly on Shive's agar than on the moist paper.

2. Rooting of excised cotyledons was observed in 41 plants belonging to 19 different families.

3. Basal halves of cotyledons rooted almost as rapidly as whole cotyledons, and apical halves were rooted in 10 species. Right and left halves of cotyledons formed roots in 16 species, and smaller fragments of cotyledons rooted in four species.

4. Shoots were developed on excised cotyledons in 22 species.

5. Seedlings, severed just above the root collar, formed new roots at the bases of the severed hypocotyls in 35 different plants belonging to 16 different families.

6. Hypocotyls severed below the cotyledons and above the root collar formed roots in four species, and shoots in four species.

7. In seedlings from which the cotyledons were removed, the plumules failed to develop.

8. Cotyledons and hypocotyls alike, form roots in either light or darkness, but some species develop best in the light, and others in the dark. The cotyledons and the hypocotyls of a given species may react differently to light.

* Papers from the Department of Botany, University of Michigan, No. 396.

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THE USE OF NON-AQUEOUS SOLVENTS IN THE STUDY OF THE RARE EARTH GROUP

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Aqueous solutions are almost invariably employed in the work which has as its object the separation of the members of the rare earth group. Differences in solubility between neighboring elements are very slight. As a result separations are slow, there are tremendous losses of expensive materials, and complete separations are almost or quite impossible. We have made a study of the solubilities of the chlorides and nitrates in various non-aqueous solvents in the hope that we might discover some solvent which has a distinctly selective action, thereby making possible more rapid, and more efficient separations. In our preliminary study we have confined our attention to anhydrous solvents and anhydrous salts. It is obvious that the greatest interest in such a study will center upon those cases in which the separations in aqueous solutions present the maximum difficulty.

Figure 1 shows the solubility of neodymium chloride in several alcohols, all of which are good solvents. The curves are regular, showing a fairly uniform increase in solubility with rising temperature. The ability to serve as a solvent increases quite regularly as we pass from the lower to the higher alcohols, methyl alcohol being an outstanding exception to this statement.

Figure 2 shows that iso-propyl alcohol is a very poor solvent for rare earth chlorides. It also shows that lanthanum chloride is slightly more soluble in both iso-propyl and propyl alcohol than is neodymium.

Figure 3 indicates that ethyl alcohol is a good solvent for lanthanum and neodymium chlorides, but in both cases the curves are not as smooth as those obtained when other alcohols are used as solvents. The behavior of ethyl chlorides indicates that complexes are easily formed. These may account for the sudden breaks in these curves. There may be some significance to the fact that at 30° both these curves drop somewhat, since similar breaks in other curves occur at about this temperature.

Ethylene glycol is a good solvent for the chlorides of neodymium and lanthanum as shown by figure 4. The curve for neodymium chloride shows a drop at 30°, but in the case of the lanthanum curve there is a marked decrease in solubility at 20°, which is followed by a surprisingly large increase at 30°. These anomalous points in the curve have been confirmed; they may be caused by the presence of a metastable state or to some other condition. It appears from these curves that the separation

of lanthanum and neodymium could be effected readily when their chlorides are extracted with ethylene glycol at 20°. This possibility is to be tested, but since these members of the group are easily separated by standard

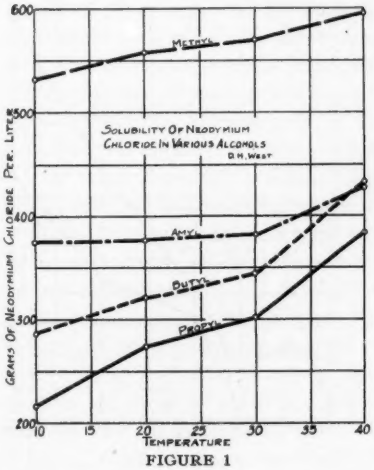

FIGURE 1

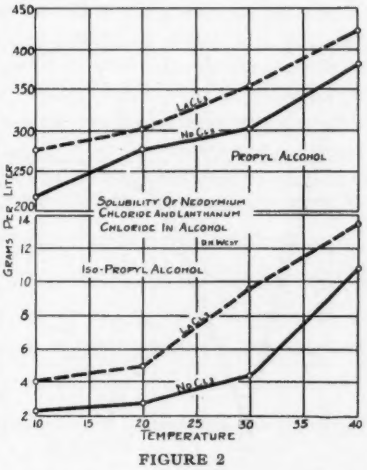

FIGURE 2

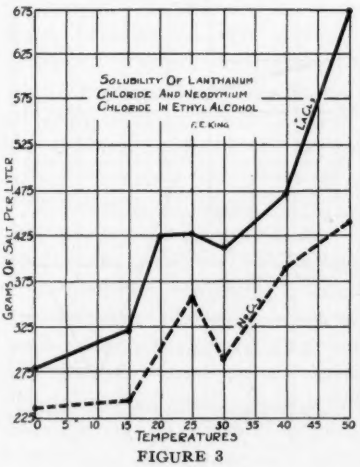

FIGURE 3

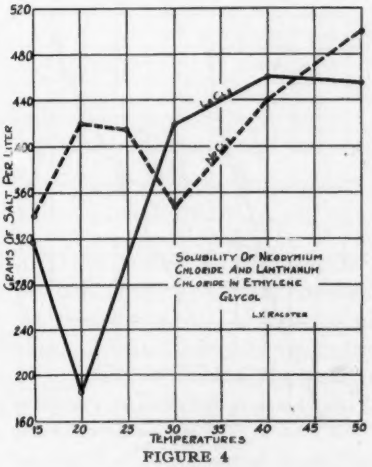

FIGURE 4

methods of procedure, there appears to be little need for such a method of separation.

In figure 5 we find a remarkable similarity in the solubilities of lanthanum and neodymium chlorides when glycerol is used as a solvent. A remarkably large dip in both curves occurs at 30°.

Turning now to the solubility of the anhydrous nitrates we find in figure 6 the atomic numbers plotted as abscissa and the solubilities at 25° as ordinates, for both dioxan and ethyl ether. It is to be observed

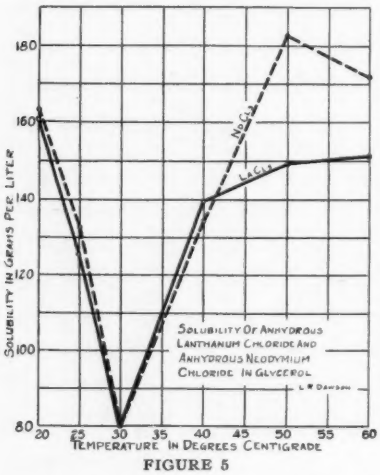
SOLUBILITY IN GRAMS PER LITER
TEMPERATURE IN DEGREES CENTIGRADE
NdCl3
LaCl3
SOLUBILITY OF ANHYDROUS LANTHANUM CHLORIDE AND ANHYDROUS NEODYMIUM CHLORIDE IN GLYCEROL
L. W. DAMSON

FIGURE 5

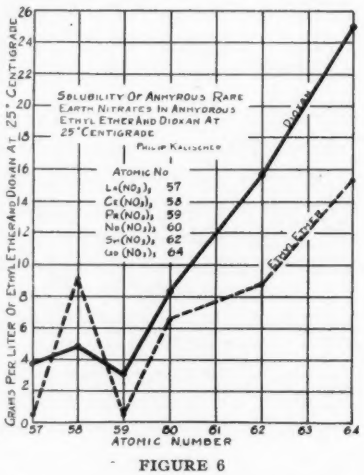

FIGURE 6

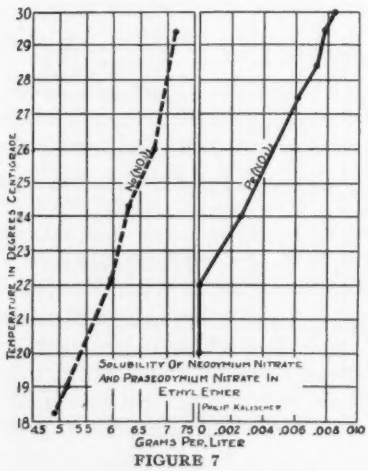

FIGURE 7

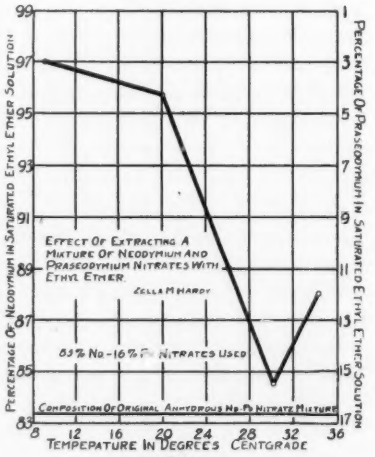
PERCENTAGE OF NEODYMIUM IN SATURATED ETHYL ETHER SOLUTION
PERCENTAGE OF PRASEODYMIUM IN SATURATED ETHYL ETHER SOLUTION
TEMPERATURE IN DEGREES CENTIGRADE
EFFECT OF EXTRACTING A MIXTURE OF NEODYMIUM AND PRASEODYMIUM NITRATES WITH ETHYL ETHER.
ZELLA M HARDY
83% Nd-16% Pr NITRATES USED
COMPOSITION OF ORIGINAL ANHYDROUS Nd-Pr NITRATE MIXTURE

FIGURE 8

that the curves are quite similar, each one showing an abnormal value for cerium nitrate. This is not surprising since cerium has many properties in which it differs rather sharply from other members of the rare earth group. The elements of higher atomic number are more soluble in these solvents than are those of lower atomic number.

Because of the difficulty of separating the neodymium and praseodymium there is unusual interest in finding a preferential solvent for one in the presence of the other. Figure 7 shows that neither is extensively soluble in ethyl ether, but that at temperatures below 22°, neodymium nitrate is slightly soluble, while praseodymium nitrate is essentially insoluble. The first attempt to utilize this difference in solubility for the separation of these elements was accomplished by using a mixture containing 83 per cent neodymium nitrate and 16 per cent praseodymium nitrate. The material was shaken for several hours with ether at various temperatures. At 30° there was only a slight enrichment in the neodymium content of the extract as is shown in figure 8. At 10° the ether soluble material contained 97 per cent neodymium, an increase of 14 per cent in one extraction.

By modifying a Soxhlet extractor in such a manner as to permit carrying out the extraction in the vicinity of 10°C., it was found to be possible to produce a rapid increase in the neodymium content of the extract. The dotted curve shown in figure 9 shows the rate at which this separation takes place in terms of the number of times the Soxhlet apparatus is permitted to siphon off. Starting with material containing 55 per cent neodymium, after one extraction the percentage has increased to 70 per cent while two extractions yield a solution containing nearly 85 per cent neodymium. If, however, the siphon is allowed to drain for fourteen times, the proportion of neodymium in the extract is noticeably less. This is apparently due to the fact that after the ether has dissolved essentially all of the neodymium nitrate in the thimble, there is some tendency to dissolve praseodymium nitrate even at the low temperature used.

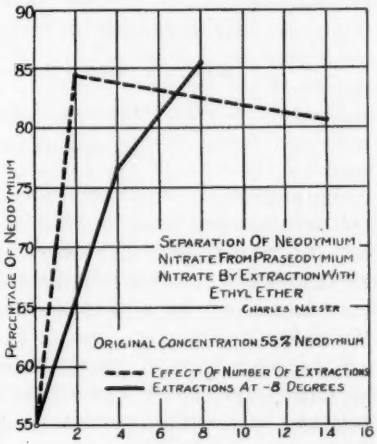

FIGURE 9

The solid curve in figure 9 shows the result of a method of fractionation by the use of our modified Soxhlet apparatus. Starting again with material containing 55 per cent neodymium an extract containing 77 per cent of this element was obtained. The solvent was then removed from the extract and the residue again extracted with ether. This second extract was found to contain about 86 per cent neodymium nitrate. By this time the fraction had become so small that a continuation of the proc-

ess was impracticable but it appeared to be possible to extract a small quantity of neodymium which was present in praseodymium. Accordingly, we selected a mixture which was composed of 94 per cent praseodymium and 6 per cent neodymium and extracted the latter with ether. The residue contained such a small quantity of neodymium that it could not be detected by spectroscopic means and we believe that this method of separation may also be applied in other cases.

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*THE DETERMINATION OF THE STRUCTURES OF THE HEXAFLUORIDES OF SULFUR, SELENIUM AND TELLURIUM BY THE ELECTRON DIFFRACTION METHOD**

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Communicated November 18, 1932

The application of electron diffraction methods in the study of gas molecules was first made by Mark and Wierl,[1] who investigated the structure of a large number of molecules in this way. Using methods closely similar to theirs, and briefly discussed in the following paragraphs, we have determined the atomic configuration and interatomic distances in SF_6, SeF_6 and TeF_6.

The Debye formula[2] for the relative intensity as a function of the scattering angle θ for x-radiation diffracted by widely separated gas molecules with random orientation is

$$I = k \sum_i \sum_j f_i f_j \frac{\sin x_{ij}}{x_{ij}}, \qquad (1)$$

in which

$$x_{ij} = 4\pi l_{ij} \frac{\sin \theta/2}{\lambda} \qquad (1a)$$

with l_{ij} the distance between the ith and the jth atoms, λ the wave-length of the incident radiation, and k a constant for given experimental conditions. The summations extend over all the atoms in one molecule. For electron diffraction the x-ray-scattering factors f_i and f_j for the atoms are replaced by electron-scattering factors ψ_i and ψ_j, which were shown by Mott[3] to be given by the expression

$$\psi_i = \frac{Z_i - f_i}{\left(\frac{\sin \theta/2}{\lambda}\right)^2}, \qquad (2)$$

in which Z_i is the atomic number of the atom and f_i, as before, the x-ray-scattering factor, essentially a function of $\frac{\sin \theta/2}{\lambda}$.

The interpretation of an electron diffraction photograph is made by comparing it with theoretical intensity curves calculated for each of several models (corresponding to different relative positions of the atoms), among which a choice can then be made. An approximate treatment can be based on the comparison of the maxima and minima shown by calculated curves obtained on substituting for f_i in Equation 1 the value Z_i (rather than ψ_i) with the apparent maxima and minima seen on visual examination of the films. The most probable model for any substance is that leading to the curve which permits the best correlation of maxima and minima with the measured diameters of the rings on the photograph. Application of Equation 1a then provides values of the interatomic distances. A complete interpretation of the photograph would require recalculation of the theoretical intensity curve with the use of the ψ-values corresponding to the interatomic distances given by the simpler treatment, and the quantitative comparison of this curve with the observed intensity curve. It has been found, however, that the very rapid decrease in intensity with increasing angle θ makes an accurate knowledge of the behavior of photographic emulsions toward electrons necessary for the interpretation of micro-photometer records of diffraction photographs. Until this knowledge is obtained, use must be made of the simpler treatment, this procedure being justified by the self-consistency of the results it leads to and by their agreement with the results of x-ray diffraction and band-spectral investigations. Wierl in this way determined interatomic distances for a large number of molecules with a probable error estimated by him at $\pm 2\%$. Our own experience supports this estimate, and indicates that still greater accuracy can be obtained by standardizing the technique of preparing and measuring the photographs.

The experiments consist in causing a well-defined beam of electrons traveling with a uniform velocity to intersect a jet of gas, the scattered electrons being recorded on a photographic film set at right angles to the direction of the initial beam. The source of electrons was a hairpin-shaped hot filament set asymmetrically in a focussing cup which could be charged to various potentials with respect to the filament. The accelerating potential of about fifty thousand volts was taken directly from the secondary winding of a transformer. The electron beam was defined by 0.2 mm. holes in two platinum foils set 130 mm. apart. The gas jet was introduced through a nozzle with a rectangular opening of dimensions 1×0.1 mm. placed with the long dimension parallel to the electron beam. The nozzle was connected through a stopcock to a small reservoir of gas maintained at a pressure of about $\frac{1}{2}$ atmosphere. The exposures in all cases were of the order of $\frac{1}{2}$ second.

A calibration of the wave-length furnished by the accelerating potential was obtained with the aid of photographs of gold. The structure of gold determined by electrons was checked by Thomson[4] with the generally accepted one determined by x-rays; hence, measurement of gold photographs constitutes a convenient method of standardization. The sharpness of the rings in the photographs used for this purpose indicated that all of the electrons were traveling with nearly the same velocity.

TABLE 1

CARBON TETRACHLORIDE

MAXIMUM	MINIMUM	x	FILM NO. 123, LIGHT $\sin\theta/2/\lambda$	FILM NO. 123, LIGHT a = C-Cl	FILM NO. 126, DARK $\frac{\sin\theta/2}{\lambda}$	FILM NO. 126, DARK a
1		0.765	0.212	1.80 Å	0.220	1.74 Å
	2	1.04	0.292	1.778	0.290	1.795
2		1.35	0.376	1.798	0.385	1.752
	3	1.69	0.474	1.784	0.484	1.746
3		2.01	0.558	1.801	0.569	1.766
	4	2.31	0.648	1.809	0.659	1.754
4		2.58	0.730	1.767	0.735	1.756
	5	2.90			0.826	1.756
5		3.215	0.905	1.777	0.905	1.777
			Weighted mean	1.788 Å		1.761 Å

SULFUR HEXAFLUORIDE

MAXIMUM	MINIMUM	x	FILM NO. 66, DARK $\sin\theta/2/\lambda$	FILM NO. 66, DARK a = S-F
1		1.05	0.310	1.69 Å
	2	1.29	0.417	1.548
2		1.51	0.506	1.491
	3	1.86	0.619	1.502
3		2.255	0.729	1.547
	4	2.70	0.907	1.49
4		3.10	1.027	1.51

Corrected value S-F = 1.58 ± 0.03 Å

SELENIUM HEXAFLUORIDE

Second maximum x = 2.250

	FILM NO. 70, DARK	FILM NO. 71, DARK
$\sin\theta/2/\lambda$	0.685	0.676
a = Se-F	1.643 Å	1.666
Corrected a	1.69 Å	1.71 Å

Average Se-F = 1.70 ± 0.03 Å

TELLURIUM HEXAFLUORIDE

Second maximum x = 2.248

	FILM NO. 80, DARK	FILM NO. 81, MEDIUM	FILM NO. 82, DARK
$\sin\theta/2/\lambda$	0.618	0.620	0.628
a = Te-F	1.819	1.812	1.789
Corrected a	1.86	1.84	1.83

Average Te-F = 1.84 ± 0.03 Å

It was found for a series of photographs made with carbon tetrachloride that the measured maxima and minima on any one photograph gave consistent values for the C-Cl separation, but that the value depended somewhat on the apparent density of the photograph. Thus the light film No. 123 and the dark film No. 126, for which data are included in table 1, lead to C-Cl = 1.79 and 1.76 Å, respectively, while very dark films lead to values as low as 1.73 Å, 4% smaller than the value C-Cl = 1.80 Å which we assume to be correct. In interpreting photographs of the hexafluorides we have compared the apparent density of each film with that of CCl_4 photographs, and have then made a corresponding

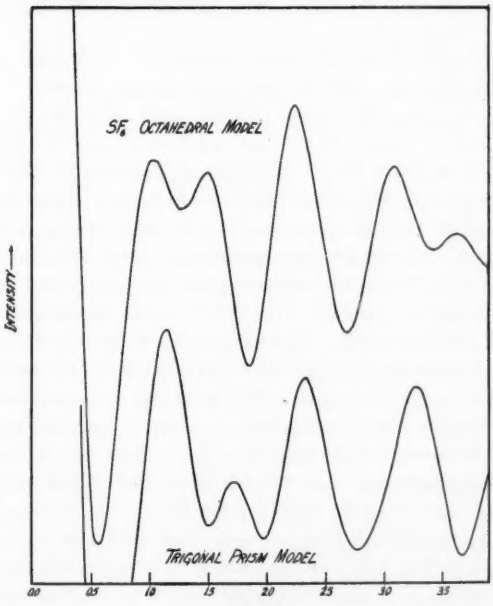

FIGURE 1

correction in the interatomic distances, which, however, was always less than 3%.

Interatomic distances obtained in this way from rather indistinct photographs made with Br_2 and Cl_2 lay within 2% of the values known from band-spectral data.

Two models were considered for each of the hexafluorides, in one the fluorine atoms being placed at the corners of a regular octahedron about the central atom, and in the other at the corners of a right trigonal prism with axial ratio unity; these were shown by Hultgren[5] to be the only

probable structures for molecules containing a central atom with six equivalent bonds. The intensity formulas used are illustrated by the following one, for the octahedral model of SF_6:

$$I/k = 2\pi Z_S^2 + 12 Z_S Z_F \frac{\sin x}{x} + Z_F^2 \left(12\pi + 24 \frac{\sin \sqrt{2}x}{\sqrt{2}x} + \frac{6 \sin 2x}{2x} \right)$$

with

$$x = 2a \frac{\sin \theta/2}{\lambda}$$

in which a is the S-F distance. The two curves for SF_6 are shown in figure 1.

The photographs from all three substances eliminate the prismatic models, the shapes and relative positions of the maxima and minima of the curves being in pronounced disagreement with the observed rings. Good agreement is obtained for the octahedral models, however. The two close inner maxima of the SF_6 curve appear as two distinct rings in the photograph. In SeF_6 and TeF_6 the increased scattering factors of the central atoms modify these two into a single broad maximum, and the photographs also show correspondingly a broad inner ring. The relative positions of maxima and minima when correlated with observed ring diameters lead to consistent values for the interatomic distances, as shown for SF_6 in the table. The error shown by the first maximum is probably due to the effect of the close second ring in causing low estimates of the ring diameter. The value 1.55 Å given by the sharp third maximum is the most reliable; this corrected by the factor 1.02 for the dark photograph leads to an S-F separation of 1.58 ± 0.03 Å. Measurements of the same sharp maximum on the SeF_6 and TeF_6 films lead to Se-F = 1.70 ± 0.03 Å and Te-F = 1.84 ± 0.03 Å.

The interatomic distances agree very well with those expected for an ionic structure. The sums of ionic radii[6] are 1.65, 1.78 and 1.92 Å, respectively, and these sums are expected to be somewhat larger than the equilibrium distances between small highly charged cations and large anions. The differences, 0.07, 0.08 and 0.08 Å, are very close to that between the observed Si-F distance 1.68 ± 0.02 Å in the crystal $(NH_4)_2SiF_6$ and the ionic radius sum 1.77 Å.

We are very much indebted to Professors R. M. Badger and C. C. Lauritsen for very valuable advice and assistance during the design and construction of the apparatus, and to Professor D. M. Yost for the preparation of the hexafluorides.

* Contribution from Gates Chemical Laboratory, California Institute of Technology, No. 345.

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*THE AGGLOMERATION THEORY OF SLEEP**

BY WILDER D. BANCROFT AND JOHN E. RUTZLER, JR.**

BAKER CHEMICAL LABORATORY, CORNELL UNIVERSITY

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Hollingworth[1] says that "normal sleep shows so many differences from the states of stupor and insensibility induced by anesthetics, narcotics and other drugs, that the resemblance between the two conditions must be regarded as superficial." Hollingworth represents a minority. Most physiologists and psychologists consider that sleep due to chloroform, morphine, alcohol and other drugs, is identical in principle with ordinary sleep,[2] though differing of course in detail. If this is true, sleep must be due in part to a reversible agglomeration of some proteins in the centers of consciousness, wherever these may be.

Many agglomeration theories of sleep have been advanced; but they have all been rejected on the ground that one would necessarily stay awake until the agglomerating agent reaches a certain concentration and would necessarily go to sleep as soon as that concentration was exceeded. Since not going to sleep is a matter of choice within certain limits, it was assumed that no agglomeration theory can be right. The flaw in the reasoning is that people have overlooked the effect due to the irritability of the sensory nerves. The more irritated these nerves are, the higher must be the concentration of the agglomerating agent necessary to overbalance the effect due to the sensory nerves and thus to produce sleep. It was a curious error to make, because everybody knows the extraordinary effect of external stimuli in keeping men awake. Laird and Muller[3] say: "Soldiers on a forced march feel they can go no farther. They are on the verge of falling by the road from sheer exhaustion. An officer comes along. He cheers them with a few words. The regimental band breaks out with a stirring Sousa rhythm—and without rest the men become refreshed and march briskly off many more miles." If the fatigue becomes great enough, it is almost impossible to keep men awake. There would come a time

when the soldiers in question would drop to the ground asleep if the company halted for a moment.

Soothing irritated nerves should and does make it possible for people to go to sleep quite regardless whether this is done by keeping the room dark and quiet or by administering drugs. It has long been the practice to give bromides either alone or in conjunction with a hypnotic. It has always been recognized that the bromide is a sedative and not a hypnotic; but people seem to have stopped there.

Of course sodium rhodanate is more effective than sodium bromide. As people grow older they usually sleep less, even though they need more sleep because they recuperate more slowly than their juniors. In many cases this inability to sleep well is due to irritated nerves and consequently we have been very successful by giving such people small amounts of sodium rhodanate in a glass of water every week or two. I take it myself and now sleep about seven hours a night instead of about four. Caffein irritates the sensory nerves and some people, including myself, cannot sleep if they drink coffee in the evening. In my own case I can counteract the effect of coffee by taking double the usual dose of sodium rhodanate in a glass of water after dinner. I have never tried this on anybody else and I have never tried putting the sodium rhodanate in the coffee. The sodium rhodanate does not put people to sleep any more than darkening the bedroom does; but it makes possible their going to sleep or staying asleep.

Our work on drug addiction has shown that there is no longer anything to fear from habit-forming drugs. In extreme cases of sleeplessness, associated with neuroses, it is possible to give hypnotics and to counteract their effect on the sensory nerves by suitable administration of sodium rhodanate. It is too soon to make a definite statement; but it looks as though sleeplessness should be a thing of the past for people who are not tuberculous and who do not have too weak hearts or kidneys.

Any method of eliminating disturbances will make it easier to go to sleep. One of my friends stops thinking when he goes to bed and goes promptly to sleep. I do not question the principle involved; but I have never been very successful in applying it. On the other hand many of us will go to sleep in the evening over certain books whereas we keep awake without any apparent effort when we play contract. Napoleon was probably a man who was always tired to the point of sleep and who had the power to ignore at will most external and internal disturbances. Consequently he could drop off to sleep at any moment. Dubois[4] believes that such people have a relatively large amount of carbon dioxide in the arterial blood; but this has not yet been proved, nor has it been proved that this is the only factor.

If the sensory nerves are too irritated, sleep becomes almost impossible.

Ordinary doses of morphine have very little effect on patients in the acute manic stage. Sodium rhodanate would probably be more effective and would certainly not have the aggravating effect on the psychosis that sodium amytal has. Dr. Gutsell has given sodium rhodanate intravenously to a man suffering from an acute attack of sciatica and the man was sound asleep inside of half an hour. Incidentally, it cured the sciatica. It sounds like foolishness to say that a man can become so tired that he cannot keep awake and yet can sometimes be too tired to sleep. The two statements refer to different conditions. If there is sufficient agglomeration of the centers of consciousness, stimulation of the sensory nerves will have very little effect. If the fatigue involves a large increase in the irritability of the sensory nerves, the man will be kept awake by these nerves, even though the fatigue of the centers of consciousness would put him to sleep under ordinary conditions.

While a little sodium rhodanate will quiet the nerves and make sleep possible, more may start peptizing the proteins of the centers of consciousness and make sleep more difficult. Various medical men have tried to repeat our experiments on the antagonism between ether, sodium amytal or morphine, and sodium rhodanate and have obtained results diametrically opposed to ours, the animals coming out of the ether, sodium amytal or morphine more slowly when given sodium rhodanate. This is just the result the medical men should get if they administered too little rhodanate, an error which they would be practically certain to make. Physicians have recently obtained good results in bringing patients out of narcolepsy by administering ephedrine, a peptizing agent. Equally good results could undoubtedly be obtained with sodium rhodanate.

An objection that has been urged against all agglomeration theories of sleep is that some people will wake with one noise and others with another; also that some people can wake pretty accurately at a given hour.[5] These are really matters of conditioned reflexes, the particular stimulus to which one is conditioned acting like a loud-speaker. My wife used to wake the moment one of the children cried, while I slept through a good deal of noise. On the other hand, I woke instantly if any of the children walked in their sleep, and my wife never heard them at all. Indians will wake at sounds and wild animals at scents that dwellers in a city would never notice, while some of us can sleep through the noise made by the milkman.

When most of us try to wake at six to catch an early train, we wake up every hour or two all through the night, showing an unregulated irritability of the sensory nerves. Why we should get these outbreaks has nothing to do with sleep, because the same phenomena can and do occur when one is awake—if one is doing something interesting and has to catch a train before the end of the evening. I know a man who has apparently an absolute sense of time. He can tell time to within about five minutes

day or night. Laird and Muller[6] say that William Jenny in London can tell the time of day or night within three minutes; but average mortals are off an hour or more. Having a clock in the room to strike the hours while we sleep increases accuracy by employing our so-called subconscious mind.

We do not know what the agglomerating substance or group of substances is. Lactic acid plays a part but apparently not the whole part. Dubois[7] thinks that carbon dioxide is the important thing; but he has not yet convinced other people. Until the physiological chemists can be of more assistance than they are now, it will be wise to designate by X the substance or group of substances which causes sleep by producing reversible agglomeration of some of the proteins in the unspecified centers of consciousness.

Having decided that X will put people to sleep unless prevented by the state of their sensory nerves, what makes people wake up? Most of us wake before we are driven to it by hunger, thirst or digestive necessities. Consequently there must be the production during sleep of an excess of some substance—possibly adrenalin—which irritates the sensory nerves enough to wake us. In the case of nightmare, it is very probably adrenalin. Let us call this hypothetical substance Y. Since wakefulness in the middle of the night can often be counteracted by sitting up in bed and reading for an hour, it looks as though the excess of Y was decomposed by the extra metabolism due to sitting up and reading.

Hibernation of warm-blooded animals differs from ordinary sleep chiefly in that the temperature regulation is thrown out of balance, the hibernating animal assuming pretty closely the temperature of his surroundings. Dubois[8] thinks that the cause of this break-down of the temperature regulation is excess of carbonic acid. Something similar is said to occur in all anesthetized animals. Leaving this out of account, the rest of it seems fairly simple to a person like myself who has no first-hand knowledge of the subject. With the fall of body temperature the rate of metabolism becomes very low and there may easily be insufficient production of Y to wake the animal. Dubois says that the marmot wakes every four or five weeks to urinate and defecate. This waking is not due to over-production of Y and the animal goes to sleep again. When warmer weather comes, the rate of metabolism goes up and the animal wakes just as any sleeping animal does. He also wakes when the temperature goes too low. My guess is that he is waked by shivering. Most of us have waked slowly at night and have taken a long time, sometimes an hour, to find out that we woke because we were chilly. Once the animal is awakened, the rate of metabolism goes up and the body temperature likewise.

Hibernation in times of drought is probably due to reversible agglomeration at the higher concentration. It is not yet clear why the rate of me-

tabolism falls off; but this is probably due to poisoning of the catalytic oxidation. The snails of the French vineyards secrete membranes[9] relatively rich in calcium phosphate which close the orifice of the shell.

An interesting question comes up in connection with psychotic patients suffering from dementia praecox catatonia. The psychosis is due unquestionably to an over-dispersed state, and we must therefore conclude either that the sleep of such patients is theoretically quite different from ordinary sleep or that the centers of consciousness may be over-agglomerated while some centers of thinking are over-dispersed. So far as I can learn, these patients do sleep normally as a rule. Consequently one portion of the brain must be over-agglomerated at times, even though another portion of the brain is over-dispersed.

Unless one identifies internal inhibition with reversible agglomeration of proteins, it is difficult to see what one can do with Pavlov's theory of sleep.[10] "Sleep and what we call internal inhibition are one and the same process. The fundamental condition of the appearance and development of internal inhibition and sleep is exactly the same. It consists in the more or less prolonged or many times repeated isolated action of a conditioned stimulus producing stimulation of the cellular structures in the cortex. In all cases of internal inhibition which were discussed in the fourth to the seventh lectures drowsiness and sleep were met with continually. In the case of extinction of a conditioned reflex some animals even at the first extinction showed not only a disappearance of the conditioned secretory and corresponding motor reaction but also a great dullness as compared with the normal state of the animal before the extinction. Repetition of extinctions, in the course of a number of days, even if all the conditioned stimuli were reinforced in between, led in every case to an obvious drowsiness and even sleep of the animal in its stand, though no such symptoms had ever previously been observed. . . .

"At this point the following question naturally arises: If sleep coincides so closely in its appearance and disappearance with internal inhibition, how is it that the latter plays such an extremely important part during the alert state of the animal, serving for the most delicate physiological mechanism of equilibration of the higher organism with its environment? To my mind all the facts which have been given in the preceding lectures dispose at once of the apparent contradiction. Internal inhibition during the alert state is nothing but a scattered sleep, sleep of separate groups of cellular structures; and sleep itself is nothing but internal inhibition which is widely irradiated, extending over the whole mass of the hemispheres and involving the lower centers of the brain as well. Thus internal inhibition in the alert state of the animal represents a regional distribution of sleep which is kept within bounds by the antagonistic nervous process of excitation."

Sleep is then due to a reversible coagulation of some of the proteins of the centers of consciousness by a substance or group of substances which we will call X and which is produced during work. The coagulating effect of X can be counteracted to some extent by the effect due to the irritability of the sensory nerves. A peptizing agent, such as sodium rhodanate, will decrease this irritability and thereby make sleep possible, though not causing it. A larger dose of the peptizing agent may act also on the centers of consciousness and thereby prevent sleep. Use is made of this when counteracting morphine.

During sleep there is excess production of a substance or group of substances which we will call *Y*—possibly adrenalin—and which irritates the sensory nerves, waking the sleeper eventually unless he is waked sooner by some other cause—hunger, thirst, digestive disturbances, light on the face, or an alarm clock, for instance.

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** ELI LILLY RESEARCH FELLOW.

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THE ZERO POINT ENERGY AND THE SEPARATION OF ISOTOPES

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Communicated November 29, 1932

The very interesting research of Washburn and Urey[1] has shown that as water is electrolyzed the residual portion grows richer in H^2. The purpose of the present note is again to point out the effect of the zero point energy on reaction rates[2] and to show that the greater zero point energy of the lighter isotope effectually aids it in passing over the potential

barriers in the surface reaction $2H^+ + 2$ electrons $= H_2$. For discussion this process may be conveniently separated into two steps. In the first step the hydrogen ion gains an electron and then becomes attached to the surface. The second step corresponds to two of these attached hydrogen atoms approaching each other so that a bond forms between them while the bond to the two surface atoms grows continuously weaker. This second process is of course simply the reverse of an adsorption process and has already been discussed in considerable detail from the point of view of quantum mechanics.[3]

Gurney[4] has considered step one as being chiefly responsible for over-

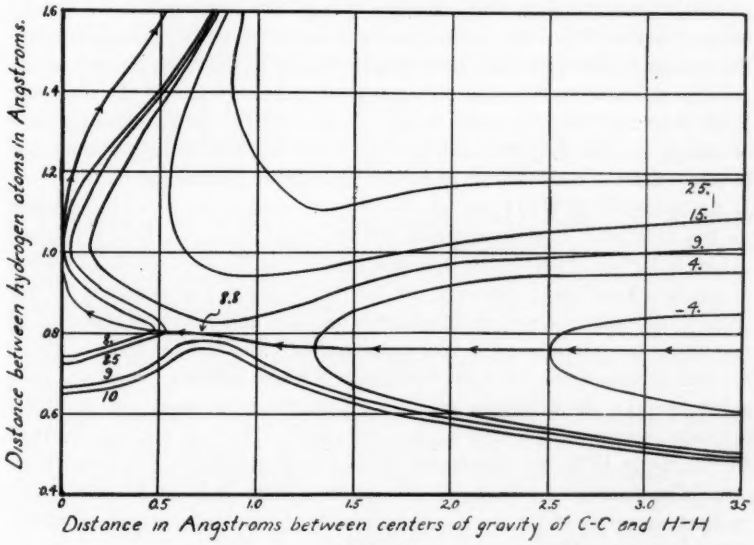

FIGURE 1

Energy contour lines in kg. cal. for the activated adsorption of H_2 on two carbon atoms 3.6 angstroms apart.

voltage. According to this theory the hydrogen ion approaches the metal surface permitting an electron to leak through an energy barrier to neutralize the ion. This point of view seems to account very well for many aspects of overvoltage. Now the nearer the ion approaches the surface the more readily an electron leaks through the thinner barrier. Thus the lighter isotopic ion having a higher zero point energy will come nearer the surface and so should be preferentially discharged. If it were not for the hydration of the ions we might expect this effect to be of considerable importance. It will, however, be practically nullified for an H_3O^+ ion. At the same time the hydrogen ion is being neutralized it is attaching

itself to a suitable atom in the surface if the surface is of a kind to provide such atoms. The second step in our process then ensues and for it the zero point energy for the oscillator, hydrogen atom-surface atom, plays a fundamental rôle.

Figure 1 is a potential energy surface taken from a paper by Sherman and Eyring[3] for the desorption of a hydrogen molecule from carbon. Such a potential surface is exactly the same for a molecule formed from either isotope of hydrogen or for a molecule formed from a mixture.

In all cases the reaction $2C—H \longrightarrow C—C + H_2$ corresponds to the system passing from a point to the left and higher up than any shown on the diagram down along the left edge, through the low point in the energy barrier (marked 8.8 kilo calories) and out along the valley paralleling the lower edge, finally yielding a hydrogen molecule. This is the reverse of the process indicated by the line with arrows in the diagram. If the molecule H^1H^1 is formed the system can finally reach an energy indicated as the zero of energy on the diagram and actually 6.2 kilo calories higher than the lowest potential in the trough of energy surrounded by the contour line -4. If the molecule H^1H^2 is formed the zero of energy is -0.8 kilo calories on the diagram. The state which the hydrogen molecule finally reaches of course has no effect on the activation energy in the electrolysis of water. A similar effect holds, however, for the hydrogen atoms attached to the surface, the different zero point energies for light and heavy isotopes being the important factors. The half quantum of vibration for CH^1 is about 4.2 kilo calories while for CH^2 it is about 3.1 kilo calories. Now the zero point energies for a system at the low point in the pass, the so-called activated state, will be very small in all cases. Thus we see that to form the molecule H^1H^2 by desorption from a carbon surface will require an activation energy of about 1.2 kilo calories more than to desorb H^1H^1. So that the latter should have a specific rate at room temperature approximately 6.3 times the latter.

The difference in activation energy for the two isotopes is much greater than the difference in the corresponding electrode voltages and the two effects are of course to be distinguished. The situation may be summarized by the statement that in reactions the heavier isotopes are slightly more inert. It should be interesting to determine whether the difference in zero point energy in step two is solely responsible for the observed isotopic separation. The zero point energy effect should permit separation by many reactions not involving electrolysis. In considering overvoltage connected with the electrolysis of gases step two should not be neglected.

The foregoing represents the theoretical approach to the problem of isotope separation as dependent on zero point energy in processes involving velocity of adsorption as one special case of the general influence of zero point energy in reaction velocity. The intimate connection between the

published data on separation by electrolysis and of desorption with the consequent necessity for different velocities of desorption, and therefore of adsorption, of isotopes at electrode surfaces was also realized by Professor Hugh S. Taylor who is arranging for an experimental test of the possibilities of separation by such processes.

[1] E. W. Washburn and H. C. Urey, *Proc. Nat. Acad. Sci.*, **18**, 496 (1932).
[2] H. Eyring and M. Polanyi, *Z. physik. Chem.*, [B] **12**, 279 (1931).
[3] A. Sherman and H. Eyring, *J. Am. Chem. Soc.*, **54**, 2661 (1932).
[4] R. W. Gurney, *Proc. Roy. Soc.* (*London*), **A134**, 137 (1931).

THE REACTION OF HYDROGEN ATOMS WITH OXYGEN AND THE HYDROGEN CHLORINE REACTION

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The rapidity with which the experimental facts connected with the photochemical union of hydrogen and chlorine change and have changed during the last century, always gives a discouraging outlook to any complete solution of the mechanism of the reaction. The results obtained during the last year, however, while still representing a comparative mobile condition, tend for the most part toward a greater simplification of the problem.

Notable among these results is the discovery in Bodenstein's laboratory[1,2] that the influence of water vapor on the reaction is not as given by the earlier work of Coehn and Jung. It is found that water vapor is without effect on the reaction. Thus is removed a difficulty which seemed to be increasingly impossible of explanation, in spite of a number of ingenious attempts.

At the symposium on photochemistry held by the Faraday Society[3] in 1931, Bodenstein pointed out that many of the facts of the reaction could be correlated in a very simple manner if we postulate the following mechanism:

(1) $Cl_2 \longrightarrow 2\ Cl$
(2) $Cl + H_2 \longrightarrow HCl + H$ $\quad k_2 = 10^{-4} \times$ no. of collisions
(3) $H + Cl_2 \longrightarrow HCl + Cl$ $\quad k_3 = 15^{-2}$
(4) $H + O_2 \longrightarrow$ $\quad k_4 = 10^{-3}$
(5) $Cl + O_2 \longrightarrow$ $\quad k_5 = 10^{-6}$
(6) $Cl + x \longrightarrow y$ or $Cl \xrightarrow{\text{Wall}} \frac{1}{2} Cl_2$

From these may be derived the equations representing the experimental results of Thon,[4]

$$\frac{d\,[HCl]}{dt} = \frac{4\,k_2k_3\,I\,\text{abs}\,[H_2]\,[Cl_2]}{OH\,(k_2k_4\,[H_2] + K_3K_5\,[Cl_2])} \qquad (1)$$

in the case where there is oxygen present in the reaction system. In oxygen-free gases, we obtain

$$\frac{d\,[HCl]}{dt} = \frac{4k_2\,I\,\text{abs}\,[H_2]}{k_6\,[x]} \qquad (2)$$

the results of Bodenstein and Unger.[5] Bodenstein then went on to evaluate the most probable values for the constants of the various reactions. From certain considerations, such as the fact that oxygen does not appreciably alter the combination of hydrogen and bromine and that the ratio of k_3 to k_4 must be about 20:1 as given by Cremer,[6] he arrives at the values of the efficiencies of these reactions given above.

He then showed that, while this scheme gives an excellent description of many of the experimental facts, there were several considerations which stood in the way of an acceptance of this mechanism as a complete picture of the reaction. One of these, the influence of water vapor on the reaction, has been removed by him as already stated. A second, the change in quantum efficiency with wave-length as reported by Allmand, seems now to be better understood in the light of the recent work of Ritchie and Norrish.[7] These authors find that hydrogen chloride has an inhibiting effect on the reaction, and suggest that it was this which caused the anomalous results reported by Allmand. A third difficulty which stood in the way of a complete acceptance of this mechanism was that reaction (4) was written in a bimolecular form but should, since it is an association reaction, involve the presence of a third body. It is the purpose of this paper to show how this third difficulty is removed by the results obtained by Dr. Lavin[8] and the author from the photoöxidation of hydrogen iodide. And in addition the value of $k_4 = 10^{-3} \times$ no. of collisions deduced by Bodenstein, is obtained from entirely independent experimental data.

According to the most generally accepted theories the mechanism of the photoöxidation of hydrogen iodide may be presented by the scheme:

$HI \longrightarrow H + I$	A	(1)
$H + HI \longrightarrow H_2 + I$	k_1	(2)
$H + O_2 \longrightarrow HO_2$	k_2	(3)
$HO_2 + HI \longrightarrow H_2O_2 + I$	k_3	(4)
$HO_2 \longrightarrow H + O_2$	k_4	(5)

The hydrogen iodide is decomposed into atoms by the action of light. The hydrogen atom so produced has two courses which it may follow. It may react with a second hydrogen iodide molecule according to (2). This is the reaction which takes place in the straight decomposition of

hydrogen iodide by light. The atom may also unite with oxygen according to (3), producing an energy rich HO_2 molecule. This molecule may then react on collision with another hydrogen iodide molecule as in (4), if it will remain stable sufficiently long. It may dissociate spontaneously (having its energy of formation still contained in the molecule) as in (5). The mean lifetime of the HO_2 molecule is given by the reciprocal of k_4. Our k_2 here is obviously Bodenstein's k_4 of the hydrogen chlorine reaction. It is upon the magnitude of the lifetime of HO_2 that the assumption made by Bodenstein, namely that the reaction of hydrogen atoms with oxygen is bimolecular, depends. If the HO_2 molecule may remain undecomposed for a sufficiently long time, the reaction is bimolecular; if dissociation occurs very rapidly, the reaction is then termolecular. A bimolecular reaction may thus be postulated if we may neglect entirely reaction (5). This is what Bodenstein has done. Experimentally this is shown to be completely justified by the work of Lavin and Bates, to which reference has already been made. This comes about from the fact that the kinetic expression which is found to represent this reaction does not involve k_4. Furthermore, the relative efficiency of the reaction of hydrogen atoms with hydrogen iodide and with oxygen is found to be 10:1 ($k_1/k_2 = 10$). The reaction of hydrogen atoms with hydrogen iodide is known to take place once in every 100 collisions. Hence the reaction $H + O_2$ takes place bimolecularly and once in every 1000 collisions, exactly as postulated by Bodenstein.

His keen analysis of the hydrogen chlorine reaction has also had support in the recent work of Rodebush and Klingelhoefer on the collision efficiency of the reaction $Cl + H_2$. It is found that this reaction goes in one every 10^5 collisions, whereas the value suggested by Bodenstein was 10^4.

The data which have accumulated in connection with the reaction do not, however, contain purely unmitigated blessings. The fact that hydrogen chloride inhibits the reaction will have to be taken into account. In addition, the work of Salley and Bates would seem to make necessary a reconsideration of the manner in which the chains of the hydrogen chlorine reaction are broken by oxygen. The chain breaking property of oxygen is usually explained by the mechanism of the reaction of hydrogen atoms with oxygen proposed by Haber:

$$H + O_2 \longrightarrow HO_2$$
$$HO_2 + H_2 \longrightarrow H_2O + OH$$
$$OH + OH \longrightarrow H_2O_2.$$

In this representation of the reaction the hydrogen chlorine chains are cut off short by the disappearance of a hydrogen atom accompanied by the formation of one molecule of water and one half molecule of hydrogen peroxide. However, Salley and Bates[9] have demonstrated that,

with hydrogen atoms produced by excited mercury atoms, it is possible to obtain 90% hydrogen peroxide in the reaction of these atoms with oxygen, a result quite incompatible with such a mechanism. They further tested an alternative process

$$H + O_2 \longrightarrow HO_2$$
$$HO_2 + H_2O \longrightarrow H_2O_2 + OH$$
$$OH + OH \longrightarrow H_2O_2$$

suggested by Frankenburger and Klinkhart[10] and showed that if these two processes could account for the high peroxide product in dry gases the reaction of HO_2 with H_2O would have to go at least 5×10^3 times as fast as the reaction of HO_2 with H_2. This would mean that if this mechanism represented the true state of affairs, small amounts of water would exert an inhibiting effect on the hydrogen chlorine reaction in the presence of oxygen. There is apparently no experimental evidence on this point.

But, in addition, it was shown that the water vapor concentration was without the effect on hydrogen peroxide formation which should be expected from this mechanism. The suggestion was made that the reaction might perhaps be better represented by the mechanism suggested by Taylor and Marshall:

$$H + O_2 \longrightarrow HO_2$$
$$HO_2 + H_2 \longrightarrow H_2O_2 + H$$

with the possible reactions ending the chains:

$$H + H \longrightarrow H_2$$
$$HO_2 + HO_2 \longrightarrow H_2O_2 + O_2$$
$$HO_2 + HO_2 \longrightarrow H_2 + 2\,O_2.$$

The chief objection to such a mechanism is the shortness of the chains involved in the reaction, as determined experimentally. (1–2.) This, however, does not make this process impossible, but shows that, if it be the correct one, the chain breaking reactions must take place with greater rapidity than the chain propagating reactions. Be that as it may, these results give room for considerable conjecture on how the hydrogen chlorine chains are actually broken by oxygen. We must realize that several reactions may take place, for example

$$\begin{aligned} HO_2 + HCl &\longrightarrow H_2O_2 + Cl \\ &\longrightarrow HClO_2 + H \\ HO_2 + Cl_2 &\longrightarrow HO_2Cl + Cl \end{aligned}$$

or those similar to the postulates of the Haber mechanism[11]

$$HO_2 + HCl \longrightarrow HOCl + OH$$
$$HO_2 + HCl \longrightarrow H_2O + ClO$$
$$HO_2 + Cl_2 \longrightarrow HOCl + ClO$$

and, in addition, no one has considered the possible chain breaking abilities of hydrogen peroxide itself:

$$H + H_2O_2 \longrightarrow H_2 + HO_2$$
$$Cl + H_2O_2 \longrightarrow HCl + HO_2$$
$$HO_2 + HO_2 \longrightarrow \text{Ending the chain}$$

In conclusion, then, it might be said that, while considerable clarification of our views of the photo combination of hydrogen and chlorine has occurred, there are many aspects of the problem which must be solved before anything like a complete picture can be obtained.

[1] Rodebush and Klingelhoefer, these PROCEEDINGS, **18,** 531 (1932).
[2] Kimball and Eyring, *J. A. C. S.*, **54,** 3883 (1932).
[3] Bodenstein, *Trans. Faraday Soc.*, **27,** 413 (1932).
[4] Thon, *Z. Physik. Chem.*, **127,** 327 (1926).
[5] Bodenstein and Unger, *Z. Physik. Chem.*, **B11,** 253 (1931).
[6] Cremer, *Z. Physik. Chem.*, **128,** 285 (1927).
[7] Ritchie and Norrish, *Nature*, **129,** 243 (1932).
[8] Lavin and Bates, *J. A. C. S.*, **55,** 81 (1933).
[9] Salley and Bates, *J. A. C. S.*, **55,** 110 (1933).
[10] Frankenburger and Klinkhart, *Trans. Faraday Soc.*, **27,** 431 (1931).
[11] Professor Bodenstein in a private communication has informed the author that the result of a study of these reactions is being published from his laboratory.

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*REVERSIBLE COAGULATION IN LIVING TISSUE. XI**

BY WILDER D. BANCROFT, ROBERT S. GUTSELL** AND JOHN E. RUTZLER, JR.

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It has been pointed out, in several of the reports[1] that have been made during the progress of the investigation of reversible agglomeration in living tissue, that sodium rhodanate antagonizes alcohol physiologically. This fact has been utilized successfully in the experimental treatment of seven cases of chronic alcoholism. Much the same theoretical and practical considerations apply here as in the treatment of morphinism. Therefore, other than to point out that at the present time it is impossible to cure the chronic alcoholic who indulges merely because of the euphoria that is produced, it is not necessary to go into the theoretical details. Sodium rhodanate will help to prevent a return to the use of alcohol by

those individuals who are nervous or sleepless when not using the intoxicant, or those with maniac depressive tendencies who cannot adjust to society adequately.

Since alcohol is easier to obtain, cheaper, less insidious and easier to break away from, than morphine, the chronic alcoholic is not deterred morally, socially and intellectually from a relapse so strongly as the morphine addict. Largely for this reason, a good prognosis is not indicated in so large a percentage of chronic alcoholics. Mark Twain said that to abstain from drinking is not to vow never to take another drink; rather to decide never to want another drink.

Case 1.—This case deals with the same person as the case of drug addiction reported in paper number ten of this series.[2] On March 18th J. H. came to us in a state of hypomania, having been in a state of alcoholic intoxication for a period of a week. He claimed that during this day he had consumed a quart of whiskey. He was dirty, dishevelled, oblivious to those around him and intoxicated. His speech was poorly coördinated; his face was gray, and exhibited nervous tension; he was thoroughly disgusted with himself. The hypomania, also an agglomerated condition, was brought on by the use of alcohol; on September 9th, the same reaction was caused by sodium amytal, another agglomerating agent. So morphine, alcohol and sodium amytal all brought about the same reaction.

Twenty grains of sodium rhodanate were given to the patient at 9:30 P. M. Bisodol was also administered. While under observation, the patient was subjected to psychotherapy without hypnosis. Thirty minutes after the sodium rhodanate was administered, the hypomanic state disappeared; and the patient was much quieter. At this time ten grains more of sodium rhodanate were given. Soon, the lines left his face and the grayish cast disappeared.

One hour after sodium rhodanate was first exhibited, the patient was entirely sober. He spoke and behaved soberly in all respects. At this time he was given Bisodol again. A bottle of whiskey was shown to him; this sickened him so that he vomited. He returned to his home cool, collected and steady. The patient took ten grains more of sodium rhodanate upon retiring, and slept well during the night. After this episode, his indulgence in alcoholic inebriety slowly subsided. Furthermore, all statements to the contrary, by unqualified professional men, the patient has not returned to the habitual use of morphine in practically one year.

Case 2.—F. P. M., 32 years of age, presented himself for treatment. For two and one-half to three years he had been a steady drinker, using about a quart of whiskey and an undetermined amount of beer each day. The patient was able to work; but he was nervous, restless and unsteady. In addition, he did not sleep well. During the twenty-four hours preceding the beginning of peptization therapy, the patient claimed to have consumed a quart of whiskey and several glasses of beer. Fifteen grains of sodium rhodanate every six hours were prescribed.

The first night after the beginning of the treatment, the patient slept uninterruptedly for nine hours. When seen during the day, he was steadier and feeling better. The patient was not given alcohol at any time. The second night he slept for eleven hours, after having had three grains of sodium rhodanate in the afternoon, and one grain at bedtime. Further than that, he dozed during the afternoon at frequent intervals; he was relaxed, and making up for some of the wear and tear on his nervous system which had occurred concomitantly with two and one-half years of agglomeration due to alcohol. The patient was steadier again than on the preceding day, happy, and

contented. So, three days after the start of peptization therapy, the signs of chronic alcoholism had disappeared. The third night he was given two grains of sodium rhodanate; he slept for eight and one-half hours. During the day he felt even better than he had the day before. The fourth night only one grain of sodium rhodanate was prescribed.

During the fourth night he slept well, and felt exceedingly well the following day. After that, he took five grains of sodium rhodanate every other night for two doses. This was followed by one five-grain dose, after which the patient used the drug only intermittently. When two weeks had elapsed, he was very well, perfectly steady and sleeping satisfactorily. Frequently he refused alcoholic beverages when they were offered to him; the patient smoked one-half of a package of cigarettes in a day, in comparison with a package and a half a day before treatment. He sat and read newspapers for hours; formerly he could concentrate only enough to read the headlines. Two months later the patient was in excellent condition.

Case 3.—I. H., 52 years old, had been a chronic alcoholic for about five years; in addition he used morphine occasionally. His initial condition was one of nervousness, sleeplessness, slight jealousy of his own comfort and an apparent need for alcohol. Nervous tension was visiblehis on face. He tended to a hypomaniac reaction in that he switched from thought to thought without completing many of them. He was distractable. Examination of the heart showed a mitral stenosis and regurgitation of long duration. This case, along with cases 4 and 6, illustrates the fact that theoretical acumen is a prerequisite to an understanding and successful application of these methods. The thing cannot be handled empirically.

The patient took ten grains of sodium rhodanate the first night and "slept better than he had for years." He was somewhat relaxed during the following day, and was given only five grains of the peptizing agent. Before retiring the second night he was given ten grains of sodium rhodanate. He did not sleep much during the night. The interesting thing here is that despite the sleeplessness the patient was calm and not at all nervous. According to the theory, this means that the "sleep center" was over-peptized; and at the same time the sensory nerves were peptized back to normal. Thus, he was sleepless but not nervous. Larger doses of the peptizing agent should result in general over-peptization, and thus uneasiness. The patient was given five grains of sodium rhodanate after breakfast, and again after lunch. This was followed by ten grains after dinner. His condition was much improved during the day; he felt very well, and appeared to be relaxed, physically and mentally. Thus, on the third day the patient was practically back to normal. He was restless during the third night, as predicted.

Throughout the fourth day the patient had no complaints; and his general condition was much improved. He was given fifteen grains of sodium rhodanate during the day. This was a reduction of five grains over the previous day. As a result, he slept better. For the next three days he remained in statu quo due to a heavy cold in the head and throat. No alcohol was administered at any time during the treatment. The first and second of these nights he slept fairly well on a total of twelve grains of sodium rhodanate during the days. On the seventh day, his cold was worse; he was not given any sodium rhodanate during the day. At night he could not sleep, and so he was given fifteen grains of the peptizing agent. A good night's sleep followed.

The rest of the treatment consisted in building up the patient, and working to determine the optimum dose of sodium rhodanate. This was finally fixed at seven and one-half grains shortly after supper. By the ninth day the patient was in comparatively excellent condition; he was calm, quiet, not nervous and relaxed. His speech was slower; and attempts to distract him failed utterly. He was sleeping satisfac-

torily. The signs of chronic alcoholism had disappeared entirely by the time he was sent home after fourteen days of treatment.

So, by following the theory and interpreting it, this patient was straightened out and his immediate problems solved. Reports received several months later indicated that he had not returned to the habitual use of alcohol.

Case 4.—H. H., 57 years of age, had been addicted to the use of alcohol for approximately forty years. The complete story of this case requires too much detail for presentation here; so, only a few of the salient features will be recorded. Upon admission to the hospital his skin was dry and flushed with acne on the nose and cheeks. The conjunctivae were injected and sore; his gums were swollen and red. There was a severe, chronic, chemical pharyngitis as a result of chronic alcoholism. The heart presented frequent extra-systoles. There was a coarse tremor of the extended tongue held in the mid-line. There was a tremor of the hands and arms. He was irritable, restless, wanted whiskey and could not sleep well.

The patient presented a definite physical and mental need for whiskey. The mental need for whiskey suggested that the chronic alcoholism was in response to a schizoid personality. Later events brought this out clearly. He was not very tractable. After six hours of observation, during which six ounces of whiskey were administered, because of lack of coöperation, the patient was given ten grains of sodium rhodanate. This did not quiet him much; two more ten-grain doses were administered before the middle of the next morning. These also failed to quiet him much. During this time, frequent small doses of whiskey were necessary to control the patient. It was considered to be unwise to dose the patient heavily with the peptizing agent because of the heart condition. The alternative was to administer sodium amytal, or some other innocuous agglomerating agent, and at the same time to reduce the amount of alcohol taken. In this way an agglomerating agent to which he had not become addicted was substituted for the one to which he was addicted. In this way he was shown that it was not necessary to have alcohol. When he realized that alcohol was not a necessity, the sodium amytal was discontinued, and his system peptized by small amounts of sodium rhodanate. Actually, sodium amytal in three-grain doses as needed to allay restlessness, was given for one day; then veronal was substituted for amytal, and administered for four days. During the next six days the patient was given seven and one-half grains of sodium rhodanate a day in divided doses. At the end of the treatment he was calm, tractable and not nervous; he slept well at night.

He was discharged with instructions to take seven and one-half grains of sodium rhodanate a day for about two weeks. Instead of following instructions, the patient took more than thirty-five and perhaps as much as sixty grains a day for five days. This over-peptized him to such an extent that he was returned to the hospital at the end of the five days suffering from an acute visual and auditory hallucinatory psychosis. He was tractable, but did not know where he was. The hallucinations were somewhat systematized. From what has preceded it is not difficult to see that agglomeration therapy was strongly indicated. During the first day he was given ten grains of veronal and three grains of sodium amytal; the second day he was given fifteen grains of veronal. On the third day he was somewhat clearer mentally. The veronal was discontinued; since the progress back to normal was slow, even with the use of an agglomerating agent, it was thought best to allow the patient to slide back to normal without agglomeration therapy other than two grains of caffeine citrate every six hours.

The patient was coherent and lucid on the sixth day; he was much improved mentally. He continued to improve during the next four days. On the tenth day he became somewhat irrational in the evening. So, a grain and a half of sodium amytal was ordered every eight hours. In order to improve his general health, and steady his nervous system more he was kept in the hospital an additional ten days. During this

time, one and one-half grains of sodium amytal were given every eight hours. The patient was in good physical and mental condition when discharged. Because of the schizoid tendency of the patient, which means that he would be over-peptized if not given artificial agglomeration, he was instructed to take a small amount of sodium amytal each day for a month or so after returning home. In five months nothing further has been heard from the case, which may mean anything.

Case 5.—M. P., 54 years old, had been a chronic alcoholic for many years. This was accompanied by nervousness, restlessness and insomnia. Upon his admission to the hospital, a particularly indulgent period of alcoholic intoxication came to an end. The patient was very much depressed; his hands trembled, and the muscles twitched. In lieu of whiskey, the patient was quieted with sodium amytal during the first fourteen and one-half hours. Six grains of the agglomerating agent were given at about midnight, four hours after admission to the hospital. At 10:30 the next morning, three grains more of sodium amytal were given. This quieted the patient in the same general manner as alcohol would have. However, when he was awake, he was nervous and restless. This shows that the sodium amytal did not bring about any essential improvement.

So, in the afternoon of the first twenty-four hours of his stay in the hospital, twenty grains of sodium rhodanate were given in a single dose. This quieted the patient somewhat; and he went to sleep again. He was nauseated in about an hour after the dose of sodium rhodanate; therefore, ten grains of sodium bicarbonate were given before each of the following doses of the peptizing agent. Two hours after the first dose of sodium rhodanate, fifteen grains more were given. This was followed by ten grains four hours later. The first two doses quieted him somewhat but he was still very restless and shaky. He became considerably more quiet after the ten-grain dose.

The patient slept most of the second evening. He grew restless around midnight; so, fifteen grains of sodium rhodanate were administered. The second night he was restless a good deal of the time, although he slept for four hours.

During the second day the patient was given fifteen grains of sodium rhodanate; he was restless and nervous in short spells. His appetite improved and he was quiet most of the day. He slept for five hours during the night. When he was not sleeping, he was not at all restless. In the morning of the third day he was very quiet, had no complaints, and was neither restless nor nervous. His hands were much steadier and the mental depression, of which he complained in the beginning, was absent. During the day he partook of the regular diet and seemed to enjoy eating. The patient passed a comfortable day. Twenty grains of sodium rhodanate were administered during the period.

The fourth night, following the third day, was passed comfortably. He was given twenty grains of sodium rhodanate during the fourth day; he was in very good condition on this day. From that time on there were no unusual occurrences. The patient slept six to eight hours a night, ate well, was not nervous or restless, and had no need for alcohol. The patient and his family stated that his recovery was attended by less nervousness, and was much more rapid, than had ever been the case on other similar occasions. The dosage of sodium rhodanate was decreased slowly so that at the end of the treatment, eleven days after admission to the hospital, he was not taking any of the drug. Upon discharge, he was instructed to use it when nervous, restless or sleeping poorly. So, in two and one-half days the patient was improved to a degree that usually required four days for attainment. He was treated for the additional time in order that his nervous system might be stabilized.

Case 6.—H. R., 43 years of age, drank in the neighborhood of ten quarts of corn whiskey in a week. The case was one of acute rather than chronic alcoholism. The patient stopped drinking two days before the services of a physician were required.

When first seen at 9:00 A. M., he behaved abnormally; he was excited, confused, talked wildly, was very nervous and definitely hallucinated. The diagnosis of delirium tremens was made immediately. In order to quiet the patient as soon as possible practicably, he was given six grains of sodium amytal. He was told that the agglomerating agent would quiet him and put him to sleep. He coöperated by lying down and attempting to go to sleep. Fifteen minutes later he arose; all of the symptoms were very much exaggerated. The reason for that state of affairs was that the sodium amytal merely acted to agglomerate further the tissues that were already agglomerated by alcohol. Enough sodium amytal would have put him to sleep, under which condition the above reaction would not have been apparent.

He left the house and walked down the road to where there was a collection of building material; there he started to build a house. Deeming him a menace, the authorities lodged him in jail. When visited professionally, just after five o'clock, he was with the other prisoners and was frightening them. He acted wildly, jumped around, yelled, laid on the floor, jumped up on the table and acted insane in all his actions. Twenty grains of sodium rhodanate were administered, by mouth as usual, at 5:30 P. M.; he was removed to the hospital. Twenty grains more of sodium rhodanate were given at seven o'clock. He then went to bed and behaved better. At this time he was very much confused; but, in contrast with his behavior earlier in the day, he was only mildly hallucinated. He was relatively quiet. Since he was not progressing so well as desired, another twenty-grain dose of the peptizing agent was given at 9:15 P. M. At this time he was behaving better than he had been.

The patient became noisy again at midnight. The theory called for more sodium rhodanate and so twenty grains more (a total of eighty grains) were administered. At 1:00 A. M. this was supplemented by thirty grains of sodium bromide, a weaker peptizing agent. He quieted down and went to sleep shortly thereafter. When seen in the forenoon he was normal mentally, quiet and not at all nervous. The patient ate heartily for the first time in a week. He passed a quiet day, remaining in bed. No more medication was given. The patient went home on the second day in good condition. This was a rather rapid recovery from delirium tremens.

Case 7.—C. D., aged 42 years, strong, well and a hard worker, was treated for acute alcoholic intoxication and insomnia. When first seen he was very nervous, belligerent and pugilistic. Under the pressure of nervousness from overwork he had reached a point where small amounts of alcohol affected him much more than usual. Twenty-five grains of sodium rhodanate were administered at three o'clock in the morning. In a short while he became less pugilistic and more tractable. About thirty minutes later he was given twenty grains more of sodium rhodanate; that made him more quiet and less nervous. In another half hour the twenty-grain dose was repeated along with a dose of sodium bicarbonate. Following that he slept and stayed in bed sleeping and resting quietly most of the day. The day after the episode, the patient was not noticeably nervous, in contrast to his condition before becoming intoxicated.

The night following the episode the patient slept better than he had for a long while; forty-five and one-half grains of sodium rhodanate were given during the day. The next night he again slept well; thirty grains of sodium rhodanate were used. There were no further signs of nervousness. Being a transient, the patient went on his way at this juncture, with instructions to use twenty grains, or less, of sodium rhodanate nightly to try to procure the desired sleep.

At different times during the past eleven months, five people have been sobered quickly after having become intoxicated with alcohol. In these cases single doses of fifteen to twenty-two and one-half grains of sodium

rhodanate were used. There was no sudden transformation from a state of intoxication to normal; but a decided alleviating effect was demonstrated.

Thus, twelve cases of alcoholic intoxication have been dealt with successfully by applying peptization and agglomeration therapy. No claim can be made, at present, that chronic alcoholism can be cured by peptization therapy; but our experience has been that, with the use of sodium rhodanate, the habit of alcoholic over-indulgence can be checked a good deal. It has been demonstrated that chronic alcoholism can be broken up and the patient returned to normal more rapidly than is usual in medical practice, if one knows the theory back of the action of alcohol. The limitations to the use of sodium rhodanate and peptization therapy are the same as those that have been found to supervene in the treatment of chronic morphinism.[3]

The general conclusions of this paper are:

1. Chronic alcoholism is benefited by treatment with sodium rhodanate, peptization therapy.
2. Such a treatment tends to return the patient to normal very quickly.
3. The patient can then sleep a normal amount and has no physical need for alcohol, provided his general condition of health does not interfere.
4. All chronic alcoholics on whom sodium rhodanate can be used safely can be cured if there is only a physical need for alcohol.
5. Since there are many nervous, mental and social causes which tend to lead to a return to alcohol, a period of close observation by the physician and the coöperation of the patient is essential in effecting a cure. Although the craving has been broken, there is nothing to prevent the patient from relapsing unless he determines not to.
6. If the need for alcohol is brought about by an inadequate personality, chronic alcoholism cannot be combated successfully with the meager facilities at our disposal.
7. Delirium tremens has been relieved effectively and quickly solely by the use of peptizing agents.
8. Single episodes of alcoholic intoxication can be dealt with to great advantage by the use of sodium rhodanate.
9. The treatment has not been, and probably cannot be, standardized.
10. The same general theory underlies the treatment as that which gave rise to a successful treatment for morphinism.

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** M.D.

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[3] Bancroft, Gutsell and Rutzler, *J. Phys. Chem.*, **36**, 2011 (1932).

BLOOD GROUP INHERITANCE IN THE RABBIT

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Domestic rabbits, as regards the composition of their blood, may be separated into groups according as they do or do not possess a particular agglutinogen. This we know from observations made by Levine and Landsteiner (1929, 1931) at the Rockefeller Institute, and from those made independently by Fischer and Klinkhardt (1929, 1930) at Frankfurt a. M., Germany, as well as from those of still other investigators named in the papers cited.

The present paper deals with the inheritance of two blood agglutinogens of the rabbit, which are transmitted as simple Mendelian dominant characters, similar to the inheritance of the *M* and *N* agglutinogens of human blood, as shown by Landsteiner and Levine (1928).

We owe the opportunity to study the genetic aspects of this problem, at the suggestion of Dr. M. R. Irwin, then National Research Council Fellow at the Rockefeller Institute, to the generosity of Drs. Levine and Landsteiner, who sent us a foundation stock of rabbits and supplied us with immune sera for our initial experiments. We are also greatly indebted to Dr. Benjamin White and his colleagues in the Antitoxin Laboratory of the Massachusetts State Department of Health for material assistance and for advice concerning serological technique. To Dr. Fischer, also, we would express our hearty thanks for samples of immune sera kindly sent to us.

Demonstration of the presence or absence of a particular agglutinogen in the blood of a rabbit may be made by the following procedure. Blood taken from a rabbit known to possess the agglutinogen is injected either directly (by transfusion) or indirectly (intraperitoneally) into one known *not* to possess it. After several such injections at intervals of a few days, the blood serum of the injected rabbit will be found to have developed an "immune agglutinin" and so to have acquired diagnostic properties. If such serum is added to blood samples of various rabbits, it will cause agglutination (clumping) of the blood cells of such individuals as possess the agglutinogen, but will not cause agglutination in those which lack it. In this way rabbits may be diagnosed and classified as possessing (+) or not possessing (−) a particular agglutinogen.

We received from the Rockefeller Institute several rabbits which had been diagnosed as negative (−), with a serum prepared by Drs. Levine and Landsteiner, and also an initial supply of their diagnostic serum. With this we were able to classify our own rabbits, though in some cases the

reaction was weak or doubtful. But using only those in which the reaction was clearly plus or minus, we found the inheritance clear cut and simple. Our own supply of serum has been produced by injecting washed blood cells from a single plus rabbit intraperitoneally into a minus rabbit bred from the Rockefeller Institute stock. The serum apparently has the same specificity as that supplied to us from the Rockefeller Institute.

When we mate together rabbits diagnosed as negative (−), we obtain only negative offspring; 134 such have been recorded. This indicates that the negative condition is recessive. From certain matings in which one parent was positive and the other negative in reaction, we obtained 133 tested offspring of which 66 were positive and 67 negative. This is obviously a 1:1 ratio, one parent (the dominant or plus one) being heterozygous, the other homozygous.

In two other matings between a positive and a negative individual, the positive parent being in one case a male, in the other a female, only positive offspring were obtained to the number of 21 in four different litters, three of which were borne by the same mother. It is almost certain that these two positive parents were homozygous dominants. Accordingly we interpret the inheritance, as did Landsteiner and Levine (1928) in the case of the *M* and *N* human blood groups, to be that of a Mendelian dominant. We shall call the gene involved in the production of this agglutinogen H_1 (*H* standing for hæmagglutinogen), to distinguish it from another, H_2, presently to be discussed. The inheritance data so far described are summarized in table 1.

TABLE 1

PROGENY OF RABBITS TESTED BY H_1 SERUM

PARENTS	PROGENY +	PROGENY −
− × −	0	134
− × + (heterozygous)	66	67
− × + (homozygous)	21	0

We are able to confirm the observation of Fischer and Klinkhardt (1930) that two differenlt aggutinogens occur in the blood of rabbits, and that there are accordingly four groups of individuals as regards the possession or non-possession of these agglutinogens. One group possesses both agglutinogens, another possesses neither, and of the other two groups, each possesses a single and a different agglutinogen. Fischer and Klinkhardt call the groups, after analogy with the four standard groups of man, *AB*, *A*, *B* and *O*. But as the correspondence of the rabbit agglutinogens is rather with the *M* and *N* of man than with the *A* and *B* (since they are demonstrable only with immune sera), it seems better to employ a different terminology.

The second blood group gene we shall call H_2. We were able to demonstrate its existence by tests made with a serum prepared by Fischer and

Klinkhardt, a sample of which was kindly sent us by Dr. Levine. Later we received a supply of serum direct from Dr. Fischer. Individuals which had given negative tests with the Rockefeller Institute serum, frequently gave positive tests with the Fischer serum and vice versa. But occasional individuals were negative with both sera or positive with both, thus giving us the four expected groups.

Dr. Snyder undertook the preparation of a continuing supply of the H_2 serum. For this purpose we sent him four individuals which were $H_1 - H_2+$ to serve as donors, and one which was $H_1 + H_2-$ to serve as recipient. With these he was able to prepare a serum identical in its properties with that supplied by Fischer, being diagnostic for presence or absence of the H_2 agglutinogen.

TABLE 2

CLASSIFICATION OF THE YOUNG PRODUCED BY VARIOUS TYPES OF MATINGS, WHEN TESTED BY BOTH H_1 AND H_2 SERA

MATING NO.	PARENTS	h_1h_2	h_1H_2	H_1h_2	H_1H_2
1	$h_1h_2 \times h_1h_2$	7	0	0	0
2	$h_1h_2 \times h_1H_2$(het.)	9	10	0	0
3	$h_1h_2 \times h_1H_2$	0	15	0	0
4	$h_1h_2 \times H_1$(het.)h_2	12	0	9	0
5	$h_1h_2 \times H_1H_2$	4	162	140	2
6	h_1H_2(het.) $\times H_1H_2$	2	67	45	40
7	$h_1H_2 \times H_1H_2$	0	51	0	52
8	h_1H_2(het.) $\times H_1$(het.)h_2	20	15	13	17
9	$h_1H_2 \times H_1h_2$	0	0	0	12
10	$h_1H_2 \times H_1$(het.)h_2	0	27	0	35
11	$H_1h_2 \times H_1h_2$	0	0	8	0
12	H_1(het.)$h_2 \times H_1H_2$	0	2	4	8
	Totals	54	349	219	166

Later, to meet the requirements of our expanding breeding experiments, we prepared other sera in a slightly different way, but having the same diagnostic properties as the Fischer serum. The method of preparing these sera will be described in more detail elsewhere.

Like the H_1 gene, H_2 is a dominant in heredity. The relations of these two genes to each other have been coming to light gradually in a series of breeding experiments, the results of which are summarized in table 2. The question is not yet fully solved, but enough is known to show that genes H_1 and H_2 are either allelomorphs or closely linked. Which of these alternatives is the correct interpretation can only be disclosed by further experiments.

In table 2, absence of an agglutinogen, as indicated by a negative reaction to the test serum, is represented by a small letter; presence of the agglutinogen, as indicated by a positive reaction, is represented by a capital letter. Absences, being recessives in heredity, are always homozygous. But a dominant may be either homozygous or heterozygous. The hetero-

zygous state, where it is known to exist in a parent, is indicated in the table, except in the case of the combination H_1H_2 which (for reasons presently to be explained) is *regularly a double heterozygote.*

In mating No. 1, double recessives are seen to breed true, as expected. In mating No. 2, one parent is a double recessive, but the other is heterozygous for gene H_2. The young are equally divided between the two parental types, as expected. Mating No. 3 is exactly like No. 2 except that the dominant parent is a homozygote. Hence all the 15 young produced are of the same type as the dominant parent. These three matings are identical in character and in the quality of their results with the three groups of matings summarized in table 1. They show that the H_2 gene is inherited as a simple dominant, in the same way that the data of table 1 show that the gene H_1 is inherited as a dominant character.

In mating No. 4, one parent is a double recessive and the other is heterozygous for H_1. The offspring are about equally divided between the two parental types, as expected. This mating is identical in character and result with the second mating listed in table 1.

Matings 5–7 require special consideration. We pass them by for the present.

In mating No. 8 a heterozygous H_2 individual is mated with a heterozygous H_1 individual. All four types of young are produced in approximately equal numbers, as expected. Mating No. 9 is between parents phenotypically exactly like those of mating No. 8, but the result is very different. Both parents are, in this mating, homozygous for the dominant gene, H_1 being borne by one parent, H_2 by the other. All the young are of a single type, double dominants. These young would, of necessity, be heterozygous for both genes, since each dominant had been received from one parent only. We have, as a matter of fact, never encountered any double dominant individuals which were not doubly heterozygous, which fact would lead one to suspect that genes H_1 and H_2 are allelomorphs, but this would not alter the numerical expectation in any of the matings thus far considered.

In mating No. 10, as in matings Nos. 8 and 9, one parent was H_1 and the other H_2 in reaction. But again the result is different. Two types of young are produced in approximately equal numbers. All the young are plus in reaction to the H_2 serum, but half of them are plus and half minus in reaction to the H_1 serum. This result indicates that the H_1 parent was a heterozygote, but the H_2 parent was homozygous.

Mating No. 11 is between parents both of which are positive in reaction to serum H_1 but negative to serum H_2. Since all the young are of the same character, it is probable that at least one parent (possibly both) was homozygous. Compare with the last type of mating in table 1.

In mating No. 12 one parent was H_1 (and heterozygous), the other a

double dominant (and, as usual, a double heterozygote). The young fall into three classes, as expected, but the numerical agreement with expectation (1:2:1) is not very close, doubtless owing to random sampling in a small population.

Mating No. 5, as first pointed out to us by Dr. Snyder, is a critical one in relation to the two alternative hypotheses (*a*) that H_1 and H_2 are allelomorphs, and (*b*) that they are closely linked but different genes. In this type of mating a double recessive individual is mated with a double dominant. If the two dominants are different allelomorphs of one and the same gene, all gametes formed by the double dominant parent should transmit either H_1 or H_2, but never *both* or *absence of both*. If so, this type of mating should produce only two types of young, H_1h_2 and h_1H_2 in character. Such individuals are indeed largely in the majority, there being 140 of the former and 162 of the latter. But we have recorded also six exceptional individuals of which four were double recessives like one parent, and two double dominants like the other parent. We have, from the first, been inclined to ascribe these rare exceptions to faulty observation, but they have continued to occur even after our technique had been carefully standardized, the sera raised to a high titre, and we were scrutinizing the results of this particular mating with especial care. In one case we made three different tests of the same blood sample, always with the same clear-cut exceptional result. Unfortunately, we are unable to make breeding tests of the genetic constitution of these exceptional individuals, for two of them, which were several weeks old when the blood tests were made, died or were lost before we were aware of their special interest, and the others were diagnosed when new-born and had already been sacrificed to furnish the required blood samples.

Mating No. 6 also produced two similar exceptions. This mating resembles mating No. 5, in that one parent is a double dominant, but differs from it in that the other parent is heterozygous for the dominant H_2, instead of being a double recessive. The expectation is, accordingly, that only three classes of young will be produced, the double recessive class being wanting, *if* H_1 and H_2 are allelomorphs. Nevertheless we have recorded two exceptional double recessive individuals from No. 6 matings.

We have, then, from matings No. 5 and No. 6 combined, eight exceptional individuals to account for, these being exceptions to the general rule that a *double dominant* individual forms only *single dominant* gametes. The exceptions represent between one and two per cent of the gametes formed by the double dominant parent. Three different explanations are possible. (*a*) Our technique in making blood tests may lack one or two per cent of being perfect. We know that occasional wrong diagnoses are made. This happened, for example, in the case of a doe which subsequently was used in breeding experiments and produced classes of young

which she should be incapable of producing in accordance with our other experimental results. A new test of the mother showed that she had originally been wrongly classified, as she was now producing young in harmony with her later blood test. The only alternative explanation possible would be to assume that she had meanwhile changed in blood group reaction. But all our other observations indicate that the blood group reactions are developed very early, even before birth, and do not subsequently change. We are more ready to believe that a mistaken diagnosis had originally been made than that the doe had changed in reaction between the two tests.

(*b*) Genes H_1 and H_2 may lie at closely adjacent but not identical loci, so that crossing-over may occur between them in a small percentage of cases. But if so, crossover double dominants should arise which would transmit genes H_1 and H_2 in the same gamete. These should constitute at least a small percentage of the normal rabbit population. But no such individuals have been discovered.

(*c*) If H_1 and H_2 are allelomorphs of the same gene, the heterozygote, which contains both of them, may produce double dominants and double recessives by non-disjunction. But this process, like that of crossing-over previously discussed, should give rise to individuals regularly transmitting H_1 and H_2 in the same gamete. But, as already stated, such individuals are unknown.

We are inclined, accordingly, to blame our imperfect technique, rather than the rabbits, for the exceptional double recessives and double dominants recorded in our experiments.

Aside from the possible production of exceptions, the No. 6 matings would be expected to produce the three classes of young regularly observed in the ratio 2:1:1. The recorded number 67:45:40 are in fair agreement with the expected ones, 76:38:38, the deviations being statistically insignificant (the greatest only 2.1 times the probable error).

The No. 7 matings, between the same phenotypes as the No. 6 matings, but with this difference, that the h_1H_2 parent was homozygous, would be incapable of producing double recessive exceptions by non-disjunction. It has produced, as expected, only young of the two classes h_1H_2 and H_1H_2 in approximately equal numbers, 51 and 52, respectively.

Consequently, in all the twelve different types of matings contained in table 2, which yielded a total of 788 tested young, close conformity is observed with the qualitative and quantitative results expected if either (1) H_1 and H_2 are different dominant allelomorphs of one and the same gene or (2) H_1 and H_2 are closely linked genes borne in the same autosomal chromosome pair. But we are inclined to favor the first interpretation rather than the second for reasons which have been stated in the discussion of the exceptional individuals recorded in matings No. 5 and No. 6 of table 2.

Levine and Landsteiner (1931) expressed the opinion that several different agglutinogens may occur in the blood of rabbits because of the observation of weak agglutinative reactions after only a small number of injections had been made into several different rabbits. But though we have made careful search for additional agglutinogens, we have been unable to find more than two. We think the fact may not be devoid of significance that blood agglutinogens thus far conclusively demonstrated occur in pairs, the A and B in man, the M and N in man, and what we call the H_1 and H_2 in rabbits. These pairs are allelomorphs of a single gene, as the existing evidence strongly suggests in the case of A and B in man, and of H_1 and H_2 in the rabbit.

Summary.—Two agglutinogens found in the blood of rabbits are inherited as Mendelian dominant characters. They are either different allelomorphs of the same autosomal gene, or closely linked; and in either case are borne in the same chromosome pair.

* This investigation has been made in collaboration with L. H. Snyder and R. D. Cameron of Ohio State University, who will report separately on the results of their experiments.

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TESTS FOR LINKAGE BETWEEN THE BLOOD-GROUP GENES AND OTHER KNOWN GENES OF THE RABBIT

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In a previous paper we have shown that two hæmagglutinogens of the rabbit (H_1 and H_2) are inherited as dominant Mendelian characters, and that they are borne in the same chromosome pair, being either allelomorphs of the same gene or (less probably) closely linked but distinct genes.

We have sought to identify the chromosome in which they are borne by studies of genetic linkage, our aim being to ascertain whether or not any other known gene of the rabbit shows linkage with the blood group genes. For if it does, we should have proof that all three are borne in the same chromosome pair.

Eight different chromosomes of the rabbit are known to contain mutant

genes. The chief identified genes which lie in these eight chromosomes are as follows:

(1) *A*, *a*, agouti vs. non-agouti. (2) *B*, *b*, black vs. brown; also *C*, *c*, color vs. albinism; and *Y*, *y*, white fat vs. yellow fat. (3) *D*, *d*, intense vs. dilute pigmentation. (4) *E*, *e*, extended vs. non-extended black pigmentation (non-extended being the same as yellow). (5) *En*, *en*, English (spotted) vs. non-English (unspotted) coat; also Du^W, du^W, self vs. white Dutch (spotted) coat; also *L*, *l*, normal vs. angora coat. (6) *F*, *f*, normal vs. furless coat. (7) R_1, r_1, normal vs. rex (short) coat; also R_2, r_2, normal vs. German rex (short) coat. (8) *V*, *v*, normal (unspotted) vs. Vienna white (blue-eyed, white) coat. With each of these eight chromosomes it is our plan to make tests for linkage with the blood-group genes.

TABLE 1

CLASSIFICATION OF THE BACK-CROSS YOUNG PRODUCED IN TESTS FOR LINKAGE OF GENE H_1 WITH THE GENES *A*, *D*, *E*, *En* AND *R*

NATURE OF THE ASSOCIATION OF H_1 WITH THE OTHER GENE	H_1 PRESENT (+)		H_1 ABSENT (−)		TOTAL	CROSS-OVERS	PER CENT CROSS-OVERS	P. E.
	A	*a*	*A*	*a*				
Coupling	30	41	32	27	130	73	56.2	2.88
Repulsion	2	3	0	2	7	4		
	D	*d*	*D*	*d*				
Coupling	22	23	30	21	96	53	55.2	3.29
Repulsion	4	2	2	1	9	5		
	E	*e*	*E*	*e*				
Coupling	26	19	30	21	96	49	50.5	3.29
Repulsion	3	3	2	1	9	4		
	En	*en*	*En*	*en*				
Coupling	115	99	106	110	430	205	47.7	1.63
	R	*r*	*R*	*r*				
Coupling	8	21	12	9	50	33	57.6	3.46
Repulsion	12	9	14	10	45	22		

We have completed tests for linkage with five of the eight known gene-bearing chromosomes with only negative results. As it may be some time before the remaining tests are completed, we desire to put on record the tests already made.

Castle (1929)[1] has described a cross made between a very large and a very small race of rabbits in a study of size inheritance. The large race bore four dominant genes (*A*, *D*, *E* and *En*) located in four different chromosomes, as is inferred from the fact that all are independent one of another in their inheritance. This race was also plus in reaction to the H_1 immune serum showing that it bore the H_1 agglutinogen.

The small race bore the four recessive allelomorphs (*a*, *d*, *e* and *en*) and was minus in reaction to the H_1 serum. Consequently, the F_1 animals

were dominant but heterozygous for all five genes *A*, *D*, *E*, *En* and H_1. A back-cross of F_1 females with the five-fold recessive small race was made as a study in size inheritance. It served also to test for linkage of H_1 with the four genes *A*, *D*, *E* and *En*, and so all available back-cross individuals were tested with the appropriate serum for presence or absence of the H_1 agglutinogen. The results of these tests are summarized in table 1, together with certain data obtained from other linkage crosses made in the study of the inheritance of the blood-agglutinogens, including special tests made for linkage with the gene for rex (short hair).

In table 1 there are no indications of linkage with genes *A*, *D* and *E*, since crossovers are in each case more numerous than non-crossovers. In the case of gene *En* (for English spotting), crossovers were in our earlier tests considerably less numerous than non-crossovers suggesting the possible existence of linkage, so we made special matings to test the matter more fully. A back-cross population of 430 individuals has now been tested. Crossovers are still less numerous than non-crossovers, being as 205:225, but the deviation from equality is now only 10, which is only 1.63 times the probable error, and so not statistically significant.

In the case of the rex character (short hair, *r*), crossovers are more numerous than non-crossovers both in the coupling and the repulsion matings, but the deviation is not of statistically significant magnitude. Hence there is no indication of linkage here. In table 1 we have combined into one category (*r*) linkage data on two different short-hair mutations, rex proper and German short-hair (Kurzhaar), since we find in experiments to be described elsewhere that these two genes are borne in the same chromosome. Consequently any gene which is linked with one of them should be linked with the other also. The evidence is negative as regards indication of linkage of H_1 with either of them.

We conclude, therefore, that the genes H_1 and H_2 lie in a chromosome other than the five which contain *A*, *D*, *E*, *En* and *R*. Whether they are found in one of the three chromosomes bearing *B* and *C*, *F* and *V*, remains to be determined.

[1] *Jour. Exp. Zoöl.*, 53, 421.

THE BEHAVIOR OF INTERCHANGE HETEROZYGOTES IN OENOTHERA

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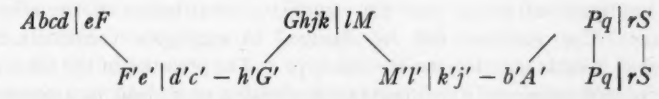
In a recent number of these PROCEEDINGS, Emerson[1] suggests that certain breeding results are incompatible with my view of the genetic structure of "complex heterozygotes" in *Oenothera*.[2] He points out, first, that crossing-over between genes is as great in the multiple rings as in the simple ring pairs and, secondly, that this crossing-over is not accompanied by interchange of non-homologous segments and consequent change of configuration in the progeny.* My view, however, is that, while certain genes, which are sometimes associated with complexes, cross over freely without interchange, the essential and permanent differences between complexes must depend upon genes which are normally incapable of crossing-over, owing to their being differently arranged in the chromosomes following structural change, and owing to their being situated next to the spindle attachment. Thus Emerson believes that the differences between complexes can be resolved into differences between independently segregating genes while I believe that they are inherently incapable of such resolution because they are associated with structural changes such as translocation, deficiency and reduplication.

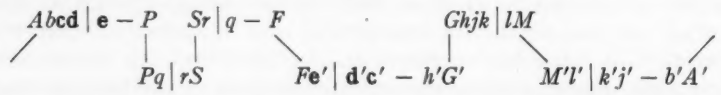
Since I put forward this suggestion new evidence bearing on the question has appeared, particularly from observation of interchange heterozygotes in maize[4] and *Pisum*.[5] In these it is found that interchange has occurred in the arms of the chromosomes at some distance from the spindle attachment. It follows in such cases, as E. R. Sansome has pointed out, that a ring of six can (and indeed must) arise from two interchanges in such a way as to give interstitial homologous "X-segments" in two chromosomes both of whose ends are non-homologous. This statement may be generalized as follows: Every successive interchange by which a ring of four is increased to six, eight and so on, will give one such new relatively translocated segment in *opposite* complexes unless two interchanges coincide.

Thus, consider a ring of four and one pair of the following segmental constitution:



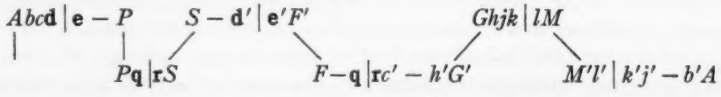
(A solidus signifies the spindle attachment and a dash, the point of interchange.) A ring of six may then arise by interchange of the *P* segment

with (1) *A*, (2) *Abc*, (3) *A'*, (4) *A'b'j'*, (5) *M'*, (6) *M*, (7) *G*, (8) *Ghj*, (9) *G'*, (10) *G'h'c'*, (11) *F'*, (12) *F*. All of these will give homologous interstitial segments in opposite complexes; (1) and (4) will be in "corresponding" segments in the ring; (2), (3), (7), (8), (9) and (10) will be in "non-corresponding" segments; (5), (6), (11) and (12) will be in overlapping segments (on both sides of the spindle attachment). For example (12) will give a zygote of the constitution:



Interchange alone therefore accounts for the apparent "translocated" segments which by later change (gene mutation, deficiency or reduplication) will give rise to the "differential segments" that I have inferred in *Oenothera*. A ring of fourteen will need to have five such "translocated" segments.

Further interchange occurring later within the ring association will likewise establish translocations but some of these will have a new type of relationship. Thus interchange between segments of chromosomes in the same complex, although having no genetic result in itself, will establish two pairs of new translocated segments each time—always in non-corresponding segments of opposite complexes. Interchange between segments in opposite complexes, on the other hand, will establish translocations in the same complex, i.e., reduplications with corresponding deficiencies. Such interchange between *S* and *G'h c'* in our ring of six will lead to a reduplication of the segments **de,** in one complex, and **qr,** in the other, in the following way:



If the segments **de** and **qr** are short their absence might be lethal to the gametes of only one sex and thus be responsible for the heterogamy that is characteristically developed in the older heterozygous species. In this connection it may be mentioned that the existence of reduplications has now been shown in *Oenothera* by the occurrence of pairing in a haploid.[6]

These various types of *primary* interchange will alter the genetic structure but they will never alter the aggregate constitution of the affected zygotes. The gametes will be changed in aggregate constitution as well as in genetic structure by the last type. The presence of the relatively translocated segments will however, by crossing-over, lead to a *secondary* interchange.[2,5] This, by altering the constitution of single gametes, which will unite with normal mates, will always give new zygotic types

in regard to aggregate constitution. The several types of recurrent mutants known to involve change of configuration (such as half-mutants and mass-mutants) correspond with these in frequency of origin and in gametic constitution. The fact that the crossing over which yields them is rare is not surprising since crossing over is regularly found to be reduced in structural heterozygotes in *Drosophila*.[7]

I conclude therefore that (*a*) the occurrence of relatively translocated segments, (*b*) their permanent separation in the history of opposite complexes, and (*c*) their association with reduplications and deficiencies within each gametic complex, all of which were inferred from the genetical and cytological properties of complex heterozygotes may now equally be inferred from the conditions of interchange under which these heterozygotes must be supposed to have arisen.

* The higher frequency of non-disjunction in maize than in *Oenothera* is also discussed by Emerson. Comparison with *Pisum* and *Campanula* shows that it can be attributed to the greater rigidity of configurations with interstitial chiasmata.[3]

[1] Emerson, Sterling, *Proc. Nat. Acad. Sci.*, **18**, 630–632 (1932).
[2] Darlington, C. D., *J. Genet.*, **24**, 405–474 (1931).
[3] Darlington, C. D., *Recent Advances in Cytology*, 142–143 (1932).
[4] McClintock, B., *Univ. Miss. Ag. Exp. Sta. Res. Bull.*, **163**, 1–30 (1931).
[5] Sansome, E. R., *Cytologia*, **3**, 200–219 (1932).
[6] Catcheside, D. G., *Ibid.*, **3** (in the press), 1932.
[7] Dobzhansky, Th., *Am. Nat.*, **65**, 214–232 (1931).

PRIME TYPES IN DATURA[1]

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Prime type is a term which has been applied to races with modified chromosomes such as are produced by segmental interchange (reciprocal translocation) and simple translocation. The prime type races of *Datura* so far found in nature have been due apparently to segmental interchange. They have been called cryptic chromosomal types[2] since their chromosomal peculiarities are hidden and without necessary effect upon the appearance of the adult plant. The term prime type is perhaps not ideal in all respects but it attempts to emphasize the fact that in these types certain of the chromosomes are abnormal when compared with those of the normal race chosen as a standard and thus would seem to have certain advantages over the term "x-normals" proposed by Brink[3] to designate similar forms in maize. Muller and Altenburg[4] and Dobzhansky[5] have

isolated prime types in the homozygous condition but they have not designated them by a special term.

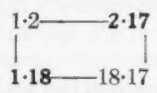
The twelve chromosomes of Line 1, which is our standard race of *Datura stramonium*, are arranged in table 1 according to their relative sizes beginning with the largest (L) as 1·2. Thus far terminal humps have been located on 8 of these 12 Line 1 chromosomes. They serve as convenient markers to identify chromosomes and particular ends of chromosomes. They are probably the equivalents of satellites or knobs which G. A. Lewitsky[6] in a study of root-tip cells of *Datura* demonstrated on several chromosomes. They are represented by superscripts at the appropriate ends of the chromosomes.

TABLE 1

$L = {}^{1}1{\cdot}2$	$M = 9{\cdot}10^{10}$	$m = 17{\cdot}18$
$l = 3{\cdot}4$	$M = 11{\cdot}12^{12}$	$m = 19{\cdot}20^{20}$
$l = 5{\cdot}6$	$M = 13{\cdot}14$	$S = {}^{21}21{\cdot}22$
$M = 7{\cdot}8^{8}$	$M = 15{\cdot}16^{16}$	$s = 23{\cdot}24^{24}$

Table 2 is a list of our prime types in which the ends of at least one of the modified chromosomes have been determined. Our standard Line 1 race is designated *PT* 1. When crossed with races whose chromosomes have the same end arrangement, the F_1 shows 12 bivalents at first metaphase in pollen-mother-cells. When it is crossed with races some of whose chromosomes do not have the same end arrangement, the F_1 shows configurations involving four or more chromosomes. Table 2 does not represent a completely random sample since recent work has been concentrated upon those types which are associated with pollen abortion. It is evident, however, that segmental interchange is by far the commonest type.

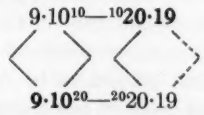
Our best analyzed prime type is *PT* 2, better known as the "*B*" race, which furnished the basis upon which the theory of segmental interchange was first proposed by Belling in 1926.[7] A separation of *B* from other races in *Datura* had been made previously by means of peculiarities in breeding behavior[8] recognized as early as 1921.[9] *PT* 2 involves an interchange between the 1·2 and 17·18 chromosomes to form the 2·17 and 1·18 chromosomes. In the heterozygous condition it forms a circle of four:



In this and other diagrams in the text the numbers representing chromosomes other than the Line 1 type are shown in boldface type.

Interchanges have been found both in nature and following radiation. In the heterozygous condition they form circles of four or six chromosomes. Circles of eight or more chromosomes have been seen only in crosses between certain of our prime types and in interspecific hybrids.

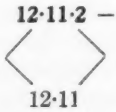
A limiting case of segmental interchange may be represented by reciprocal interchange of *only* the humps. In the heterozygous condition it forms a configuration different from the circle of four due to segmental interchange. Two bivalents are attached at the hump region only. Since one of the bivalents is frequently open distally to the humps, the configuration has the appearance of a necktie. This "necktie" has also been described as a "figure of eight"[10] but the latter designation has caused confusion since it has been used by others[11,12] in a different sense. The type of this sort from nature which has been found in *Datura stramonium* is *PT* 7. In its origin apparently an exchange of humps between the $9{\cdot}10^{10}$ and $19{\cdot}20^{20}$ chromosomes took place to produce the $9{\cdot}10^{20}$ and $19{\cdot}20^{10}$ chromosomes. In the heterozygous condition it forms a "necktie" of four chromosomes as follows:



The diagrams in figure 1 show our explanation of the cytological picture of heterozygous *PT* 7 and of the 50 per cent pollen abortion associated with this sort of interchange. The ·19 ends are usually open as shown by the dotted lines and thus give to the configuration the appearance of a necktie.

This sort of interchange which produces a "necktie" in the heterozygous condition has been found both in nature and following radiation. Thus far cases of six or more chromosomes united in the hump region have been seen only in crosses between certain of our prime types. Sometimes the union between the bivalents at their humps fails to take place. A P.-M.-C. then, instead of showing ten bivalents plus a "necktie" of four chromosomes, shows twelve separate closed bivalents. In fact this configuration is easily missed if a superficial examination only is made and was not observed in an earlier study when a configuration of four chromosomes was expected.[13]

Simple translocations have been found only following radiation. A chromosome breaks into two fragments, one of which remains free, the other of which becomes attached to a host chromosome. In the formation of *PT* 6, for example, the 1·2 chromosome was broken in two; the ·1 fragment remained free, the ·2 fragment became attached to the ·11 end of the 11·12 chromosome. This free fragment (·1) has the spindle fibre which belonged to the original 1·2 chromosome which was broken. The attachment of the ·2 fragment to the 11·12 host chromosome does not prevent the functioning of the terminal attachment point at the ·11 end. In the heterozygous condition it forms a "kite" of four chromosomes as follows:



This description of *PT* 6 applies equally well to other simple translocations. *PT* 5 and *PT* 6 which were isolated from the same translocation will be discussed more fully in a separate paper. The products of this translocation have been utilized in the synthesis of two of the pure-breeding types with extra chromosomal material to be discussed in the succeeding paper.

Prime types have been obtained from nature and following radiation treatment. An examination of 549 races of *D. stramonium* from nature yielded only five prime types. These are listed in table 2 as *PT*'s 1, 2, 3, 4 and 7. *PT* 1 is the predominant type in the United States and Brazil, *PT* 2 elsewhere. In addition, our tester races of *D. ferox*, *D. quercifolia* and *D. leichardtii* have been proved to be *B* races.[10] *PT* 3 is almost entirely confined to the west coast of South America, all the purple plants tested from this region being *PT* 3's. *PT* 4 and *PT* 7 occur in races from North and Central America, Southern Europe and Africa. A single race may have the modified chromosomes characteristic of several prime types. Thus we have races which may be classified as belonging at the same time to *PT*'s 2, 4 and 7.

By means of intra se crosses, cryptic prime types have been demonstrated in *D. innoxia*, *D. meteloides*, *D. metel*, *D. leichardtii* and *D. quercifolia*.[10] The first three species will not cross with *D. stramonium*, but an indirect method of isolating their prime types in terms of *D. stramonium* has been used with the first two. Fortunately *D. leichardtii* acts as a bridging species. By repeatedly back-crossing *D. ferox*, *D. quercifolia* and *D. leichardtii* to *D. stramonium*, it has been possible to obtain races which, except for the modified chromosomes of the prime types involved, have only Line 1 chromosomes. Thus we have secured the equivalent of homozygous *PT* 2 from *D. ferox*, *D. quercifolia* and *D. leichardtii*, and the equivalent of *PT* 3 from *D. ferox* and *D. quercifolia*.

The spontaneous occurrence of segmental interchange leading to the formation of prime types is not only relatively rare in nature but has been infrequent also in our controlled cultures of *D. stramonium*. None were found in 22 sublines derived from primaries and secondaries although a few tertiaries, presumably due to segmental interchange, have been obtained from Line 1. As a result of radiation treatment, however, an abundance of prime types has been obtained.

Usually a prime type is first identified in the heterozygous condition. If differential viability does not interfere, its progeny will be as follows:

1 homozygous Line 1 (12 *BV*) + 2 heterozygous *P.T.* (configuration) + 1 homozygous *P.T.* (12 *BV*). The 12 bivalents are selfed and back-crossed to Line 1. That 12 bivalent plant which induces the configuration in the back-cross progeny is homozygous for the prime type.

Rarely a prime type can be recognized in the homozygous condition at meiosis by changes in the size and shape of the modified chromosomes. In a few homozygous prime types due to segmental interchange the modified chromosomes show a distinct change in size. In *PT* 11, for example, the 14·18 chromosome is much smaller than the smallest Line 1 chromosome. In a homozygous prime type due to translocation the free fragments can be recognized as rod-shaped chromosomes attached at one end only in contrast to the usual V-shaped chromosomes attached at both ends. These two fragments show no attachment with each other at that end which represents the place where the original chromosome was broken. The attached fragments show as a projection from the closed bivalent formed by the host chromosomes.

Compensating types[14] may be used in the isolation of prime types from the heterozygous condition when one or more of the modified chromosomes are known. The appropriate compensating type is used as a female in crosses to the heterozygous prime type in question. Among the compensating types in the resulting progeny one heterozygous for the prime type is determined cytologically. The functional pollen of such a plant transmits only the prime type. The 2*n* offspring of such a compensating type therefore will be homozygous for the prime type involved. Compensating types are now known for eight of the twelve chromosomes in *Datura*.

The association of more or less definite proportions of aborted pollen grains with the heterozygous condition of certain prime types may assist in their isolation without recourse to cytological study. Prime types which induce pollen abortion are also being used as testers with which to locate genes in particular chromosomes.

In table 2 the percentages of pollen abortion induced by the various prime types when they are heterozygous should be considered as provisional only. These estimates may be changed after the races have been further purified. Genes are known which affect the amount of pollen abortion. Environmental influences also affect the percentage of aborted grains. *PT* 3 when heterozygous is quite variable when grown in the greenhouse. Sometimes it induces only good pollen or sometimes 50 per cent abortion, although usually showing about 25 per cent of aborted grains when grown in the field. Among the prime types listed in this table, more than a third do not induce pollen abortion when they are heterozygous. "Necktie" configurations are usually associated with 50 per cent abortion as explained by figure 1. Circles and "kite-like"

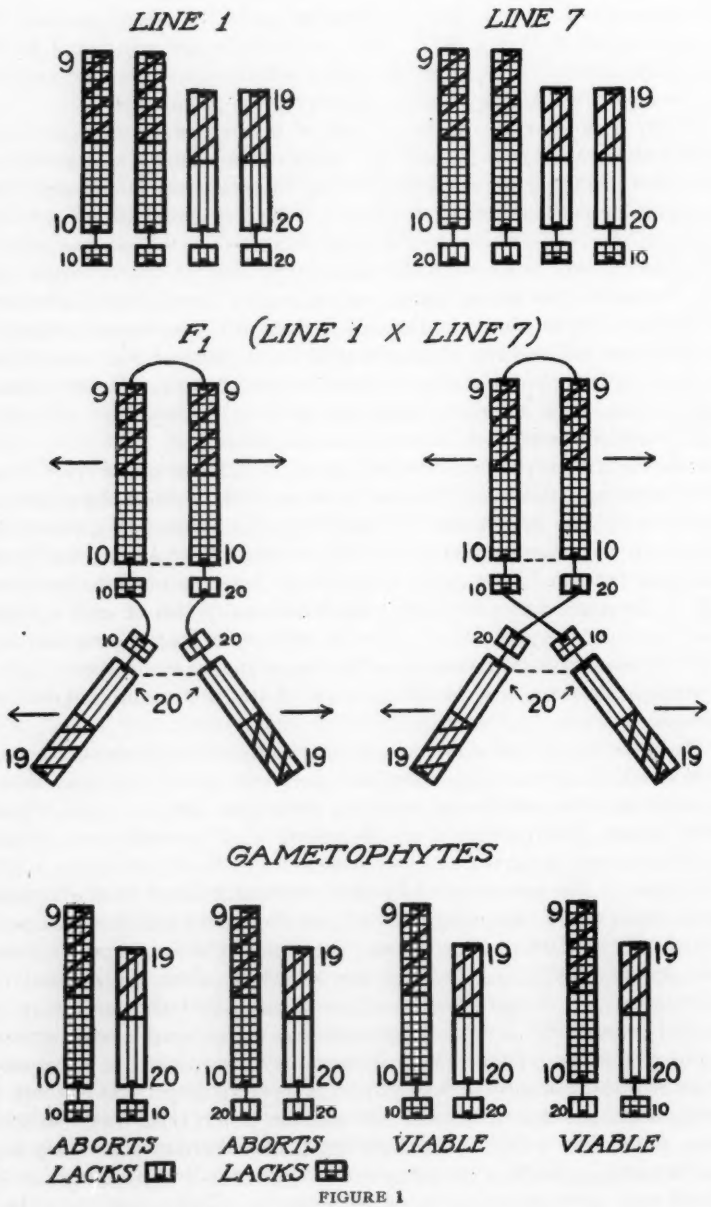

LINE 1
LINE 7
F1 (LINE 1 X LINE 7)
GAMETOPHYTES
ABORTS LACKS
ABORTS LACKS
VIABLE
VIABLE

FIGURE 1

configurations may or may not be associated with pollen abortion. Since configurations of four or more chromosomes usually show the chromosomes arranged on the spindle in zigzag fashion, alternate chromosomes tend to go to the same and adjacent ones to opposite poles. Viable gametophytes therefore are to be expected. A circle or chain, however, may break up into pairs of chromosomes attached to one another at one end, or the end members of a chain may break away. Such irregularities at late metaphase may disturb the precision of the orderly disjunction effected by the zigzag arrangement and thus produce non-viable gametophytes.

Mention may be made here of the semi-sterile strains of corn which Brink,[3] Burnham,[15] and their associates have investigated. In each case 50 per cent of pollen abortion is associated with a heterozygous, circle-inducing prime type. The chromosomes in these circles are not arranged on the spindle in zigzag fashion, hence adjacent chromosomes may go to the same pole. Since these types were selected first as pollen abortion inducers, and the cytology investigated afterward, they may not represent a random sample of the prime types in corn.

Modified chromosomes in prime types were at first identified by means of $2n + 1$ primaries rendered heterozygous for the prime type under investigation. Heterozygous *PT* 3 for example, shows a chain of five chromosomes, instead of four, when either the 11·12 (*M*) or the 21·22 (*S*) chromosomes are present as extras. Therefore the 11·12 and 21·22 chromosomes are involved in this interchange. The ends of the modified chromosomes are determined by crosses with such secondaries as are available. Thus the secondary $2n + 11{\cdot}11$ when heterozygous for *PT* 3 shows a circle of five chromosomes in the following order:

$$- S^{\circ} - M - 11{\cdot}11 - M - S -$$

The 11·11 chromosome was identified by a tendency to bend back on itself to form a "doughnut," characteristic of secondary chromosomes. It was found in the circle *between* the two *M*-sized chromosomes, one of which was known to be 11·12. Therefore the other *M*-sized chromosome must be a modified *M*, one end of which is ·11. Also since the ·12 end of the 11·12 chromosome lies next to an *S*-sized chromosome, one end of the latter must be ·12. Since we have no secondaries of the 21·22 chromosome, it is necessary to use other means of identification. Thus the ·21 end of the 21·22 chromosome has a terminal hump. In the circle of five the ° represents the joint humps of the ·21 ends of the *S* (21·22) chromosome and the adjacent *M* which must be a modified chromosome. Therefore this end of the modified *M* is ·21. Since the other end has been determined as ·11, this modified *M* is 11·21. The modified *S*, one end of which has been determined as ·12, is 12·22. Therefore the circle of four which *PT* 3 induces may be expressed as follows:

(*M*) 12·11——**11·21**° (*M*)
| |
(*S*) **12·22**——22·21° (*S*)

Except for the 21·22 and 23·24 chromosomes, for each of which a terminal hump identifies one end, there is at least one secondary for each of the twelve chromosomes. The ultimate determination of all prime types whose modified chromosomes involve these ten chromosomes is made by means of the secondaries of Line 1.

Figure 2*A* is a diagram illustrating the method of using the position of a secondary in a configuration to determine the end of a modified chromosome. In this case the secondary 1·1 chromosome was used to determine the ·1 ends of the *L* and *m* chromosomes to which it was

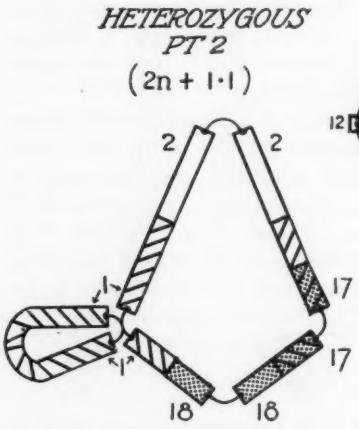


FIGURE 2A

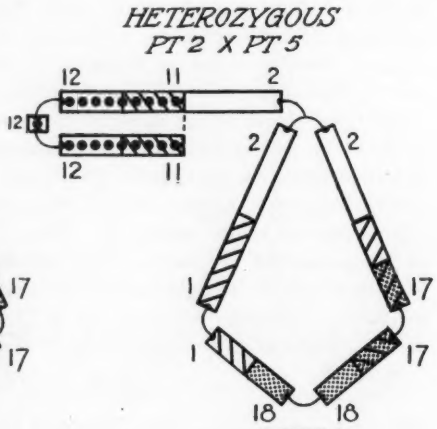


FIGURE 2B

attached, in a way similar to that in which the 11·11 chromosome was used to identify ends in *PT* 3 discussed above.

The use of $2n + 1$ types is tedious, however, since only a part of the offspring carry the extra chromosome. After the modified chromosomes of the first few prime types had been determined, they were used as testers for identifying the modified chromosomes of newly isolated prime types. For example, *PT* 10 crossed with *PT* 16 gives an F_1 which shows two separate circles of four chromosomes each. *PT* 10 crossed with *PT* 2 however gives an F_1 which shows one circle of six chromosomes. The presence of a circle of six in the latter case instead of two circles of four is due to the fact that the same 1·2 chromosome is involved in both interchanges. Figure 2*B* is a diagram of the cross between *PT* 2 and *PT* 5. The ·2 end of the 2·11·12 chromosome connects in the circle of four

between the two *L* chromosomes, showing that here are the ·2 ends of these chromosomes.

By a careful selection of prime types we can test for all twelve chromosomes. As a matter of routine, all newly isolated prime types are crossed to the selected list of testers. A tester is more useful if the modified chromosomes show some morphological peculiarity in size or shape or the position of a terminal hump. At present we are using the following testers: *PT*'s 4, 7, 9, 10, 11, 33 and 40. *PT*'s 9 and 10 are combined in one race, so that this one race can be used to test for four chromosomes at once. We are making crosses to combine *PT*'s 4 and 7 and also *PT*'s 33 and 40. When this is done we will have in only four races, chromosomal testers with which to identify the ends of all twelve chromosomes.

In table 2 the modified chromosomes of several prime types are designated by the same numbers, even though they are of distinctly different origin. In this connection it should be remembered that the numbers refer only to the *ends* of the chromosomes. Frequently the locus of a break cannot be determined cytologically in metaphase chromosomes. However we do know in the case of *PT* 10 and *PT* 25, whose modified chromosomes bear the same numbers, that these two prime types are not identical. When crossed together, the F_1 shows 12 closed bivalents but the two components of both the *L* and of an *M*-sized bivalent are unequal in size. Obviously the breaks in the 1·2 and 13·14 chromosomes occurred at different loci in the origin of these two prime types.

Plants which are prime types may or may not be morphologically distinct. Most of them are not, and hence have been called "cryptic types." However a few obtained from radiation treatment are distinct, possibly in some cases because of excess chromosomal material present as is true of *PT* 5, or possibly in other cases because of "genes," if such they are, which are closely linked with the modified chromosomes. Both dominants and recessives appear to be associated with the prime type chromosomes. *PT* 6 is associated with an "open type," *PT* 34 with "zigzag," *PT* 44 with "rough 5" and *PT* 51 with "Rough 4." These morphological types are being investigated further.

Table 2 lists 53 prime types. *PT* 1 is the standard Line 1. Thirty-four induce circles when crossed to Line 1, five induce "neckties," twelve induce "kite-like" configurations. The circles and "neckties" are induced by prime types which are the result of segmental interchanges; the "kite-like" configurations are due to translocations. *PT*'s 15 and 31 are listed both as circle and "necktie" inducers. Their peculiar behavior may be explainable after a detailed study of the 3·4 chromosome has been made. In *PT*'s 15, 18, 19 and 22, the italicised ends of modified chromosomes indicate union between them by these ends. All involve the 3·4 chromosome. Where the modified chromosomes are of different size from those

TABLE 2

PRIME TYPES IN DATURA

PT	× L1	L1 CHROMOSOMES INVOLVED	POLLEN ABORTION IN F_1	MODIFIED CHROMOSOMES	FIRST PEDIGREE	ORIGIN
1	BV		OK		S. I. *L*1	Nature
2	⊙ 4	*L*-1·2 *m*-17·18	OK	*L*-2·17 *m*-1·18	"B" S. I. 4	Nature
3	⊙ 4	*M*-11·12 *S*-21·22	±25%	*M*-11·21 *S*-12·22	S. I. 224	Nature
4	⊙ 4	*l*-3·4 *S*-21·22	OK	*l*-4·22 *S*-3·21	S. I. 442	Nature
5	Tr. 4	*L*-1·2 *M*-11·12	OK	*L*-12·11·2	27377(1)	Radium
6	Tr. 4	*L*-1·2 *M*-11·12	OK	*L*-12·11·2 *m*-·1	27377(1)	Radium
7	∞ 4	*M*-9·10^{10} *m*-19·20^{20}	±50%	*M*-9·10^{20} *m*-19·20^{10}	S. I. 7	Nature
8	∞ 4	*M*-9·10^{10} *M*-11·12^{12}	±50%	*M*-9·10^{12} *M*-11·12^{10}	270316(100)	Radium
9	Tr. 4	*m*-19·20 *s*-23·24	±25%	*M*-20·19·23 *s*-·24	281284(7)	X-ray
10	⊙ 4	*L*-1·2 *M*-13·14	OK	*l*-1·13 *l*-2·14	281284(7)	X-ray
11	⊙ 6	*M*-11·12 *M*-13·14 *m*-17·18	±25%	*l*-12·17 *M*-11·13 *s*-14·18	270316(278)	Radium
12	⊙ 4	*M*-13·14 *s*-23·24	OK	*M*-13·23 *s*-14·24	27377(1)	Radium
13	⊙ 4	*L*-1·2 *M*-9·10	OK	*L*-1·9 *M*-2·10	281031(7)	Radium
14	⊙ 4	*M*-11·12 *M*-13·14	OK	*M*-11·13 *M*-12·14	281284(1)	X-ray
15	⊙ 4 ∞ 4	*l*-3·4 *M*-15·16	±50%	*l*-3·*15* *M*-4·16	281283(3)	X-ray
16	⊙ 4	*M*-7·8 *S*-21·22	±25%	*M*-8·22 *S*-7·21	281038(7)	Radium
17	⊙ 6	*M*-9·10 *M*-13·14 *s*-23·24	±15%	 *M*-14·23	281284(4)	X-ray
18	Tr. 4	*l*-3·4 *m*-17·18	±50%	*l*-3·*4* *m*-17·*18*	281283(1)	X-ray
19	Tr. 4	*l*-3·4 *M*-13·14	±25%	*l*-3·4 *M*-13·*14*	281284(5)	X-ray
20	⊙ 4	*M*-11·12 *M*-15·16	OK	*M*-11·15 *M*-12·16	281283(2)	X-ray
21	⊙ 4	*M*-7·8 *M*-13·14	±15%	*M*-7·13 *M*-8·14	281030(22)	Radium
22	Tr. 4	*l*-3·4 *M*-13·14	±50%	*l*-3·4 *M*-13·14	281283(5)	X-ray
23	Tr. 4	*L*-1·2 *M*-9·10	±50%	*L*-*x*·*y*·9 *m*-·10	2901045(28)	Radium
24	⊙ 4	*M*-15·16 *M*-	OK		2901049(18)	Radium
25	⊙ 4	*L*-1·2 *M*-13·14	OK	*L*-2·14 *M*-1·13	2901049(25)	Radium
26	⊙ 4	*M*-11·12 *M*-13·14	±25%	*l*-12·13 *m*-11·14	2901050(25)	Radium
27	⊙ 4	*l*-3·4 *s*-23·24	OK	*l*-3·23 *s*-4·24	2901050(25)	Radium
28	⊙ 4	*M*-9·10 *m*-17·18	±25%	*M*-9·18 *m*-10·17	2901055(1)	Radium
29	∞ 4	*M*-7·8^{8} *M*-9·10^{10}	±50%	*M*-7·8^{10} *M*-9·10^{8}	2901048(22)	Radium

TABLE 2 (*Continued*)

PT	× *L*1	*L*1 CHROMOSOMES INVOLVED	POLLEN ABORTION IN F_1	MODIFIED CHROMOSOMES	FIRST PEDIGREE	ORIGIN
30	⊙ 4	*M*-13·14 *s*-23·24	±25%	*M*-14·23 *s*-13·24	2901041(1)	Radium
31	⊙ 4 ∞ 4	*l*-3·4 *M*-	OK		2901071(3)	Radium
32	Tr. 4	*M*-9·10 *M*-11·12	±50%	*l*-11·12·9 *s*-·10	2901047(15)	Radium
33	Tr. 4	*M*-7·8 *M*-15·16	±50%	*l*-7·8·15 *S*-·16	2901056(30)	Radium
34	∞ 4	*M*-11·12[12] *s*-23·24[24]	±50%	*M*-11·12[24] *s*-23·24[12]	281283(9)	X-ray
35	⊙ 4	*M*-9·10 *M*-11·12	OK	*M*-9·12 *M*-10·11	291055(1)	X-ray
36	Tr. 6	*l*- *M*-13·14 *M*-	±50%		291056(2)	X-ray
37	⊙ 4	*l*-3·4 *m*-17·18	±25%	*l*-4·17 *m*-3·18	2901052(12)	Radium
38	Tr. 4	*M*- *S*-21·22	±50%	*l*-*x*·*y*·22 *s*-·21	291054(1)	X-ray
39	⊙ 4	*M*- *m*-19·20	OK	*l*-*x*·19 *s*-*y*·20	291054(1)	X-ray
40	⊙ 4	*l*-5·6 *m*-19·20	OK	*l*-5·20 *m*-6·19	281283(7)	X-ray
41	⊙ 4	*l*-3·4 *M*-7·8	OK	*l*-4·7 *M*-3·8	2901049(3)	Radium
42	∞ 4	*L*-2·1[1] *M*-15·16[16]	±50%	*L*-2·1[16] *M*-15·16[1]	291053(1)	X-ray
43	⊙ 4	*M*-7·8 *M*-15·16	OK	*M*-7·16 *M*-8·15	2901055(26)	Radium
44	⊙ 4	*M*-7·8 *M*-15·16	±25%	*M*-7·16 *M*-8·15	291057(1)	X-ray
45	⊙ 4	*L*-1·2 *M*-15·16	OK		281284(1)	X-ray
46	∞ 4	*L*- *m*-19·20	±25%		2901046(17)	Radium
47	⊙ 4	*M*-7·8 *M*-13·14	±25%	*l*-7·14 *m*-8·13	2901038(4)	Radium
48	⊙ 4	*L*-1·2 *m*-	±25%	*l*-1·*x* *m*-2·*y*	2901056(24)	Radium
49	⊙ 6	*l*- *M*- *m*-19·20	±25%		2901063(9)	Radium
50	⊙ 4	*M*-7·8 *m*-19·20	±15%	*M*-7·20 *m*-8·19	291058(2)	X-ray
51	⊙ 4 Tr. 4	*L*-1·2 *M*-11·12	±50%		2901061(6)	Radium
52	Asym. bv.	*M*-7·8	±50%		270316(288)	Radium
53	⊙ 4	*M*- *m*-19·20	OK		2901055(18)	Radium

of Line 1, as in *PT* 11, this change is indicated by a change in size classes. *PT* 51 is listed as an inducer of both a circle and a "kite-like" configuration. Further study is needed to determine the exact nature of this translocation. Furthermore we do not yet understand what has happened to the 7·8 chromosome in *PT* 52.

These 53 prime types may be arranged according to the Line 1 chromo-

somes involved in the modifications. Thus the 1·2 chromosome is involved in eleven prime types, the 3·4 in nine, the 5·6 in one, the 7·8 in ten, the 9·10 in nine, the 11·12 in twelve, the 13·14 in thirteen, the 15·16 in eight, the 17·18 in five, the 19·20 in eight, the 21·22 in four, and the 23·24 in six prime types. This list is incomplete because the identification of the modified chromosomes has not been completed for nine of these *PT*'s. Nor should the list be considered as a random sample. Thus the 5·6 chromosome has been identified in only *PT* 40 because previously we have had no routine prime type tester for this chromosome. It was necessary therefore to depend upon the secondaries of $2n + 5{\cdot}6$ as testers for this chromosome. There is evidence that at least two of these nine unfinished prime types probably involve the 5·6 chromosome.

In addition to this list of 53 prime types in table 2, we have 27 more which are not listed because none of the modified chromosomes have been identified. Of these, seventeen are circle inducers, four "necktie" inducers, five inducers of "kite-like" configurations and one induces two asymmetrical bivalents similar to *PT* 52. Combining the two groups, out of a total of 80 prime types, 51 (63.8%) are circle inducers, nine (11.2%) "necktie" inducers and seventeen (21.3%) induce "kite-like" configurations. Furthermore if those prime types be included which have not yet been isolated in the homozygous condition, we have well over a hundred prime types of various kinds in our collection.

These prime types have been of value as chromosomal testers to identify the ends of chromosomes which have been modified by radiation treatment and of the interchanged chromosomes in the races of *Datura stramonium* found in nature. They are being used in an attempted analysis of the chromosomal changes which have taken place in the other species of *Datura*. Prime types which induce pollen abortion as well as those which are distinguished by peculiarities in morphological appearance are of value in locating genes in particular chromosomes. Furthermore, the modified chromosomes in prime types furnish material for compensating types and from the latter, pure-breeding types with extra chromosomal material have been synthesized. By studying the morphological effects of extra chromosomal material in the form of fragments and interchanged chromosomes from prime types, it is possible to gain information concerning the normal genic constitution of different parts of the chromosomes. Prime types, in short, are of value in a study of the nature of chromosomes and of chromosomal evolution.

[1] Some of the prime types discussed in the present paper were found by Mr. J. S. Potter under a grant from the NATIONAL RESEARCH COUNCIL, Committee on the Effects of Radiation on Living Organisms.

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METHODS OF SYNTHESIZING PURE-BREEDING TYPES WITH PREDICTED CHARACTERS IN THE JIMSON WEED, DATURA STRAMONIUM

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By means of primary, secondary and tertiary $2n + 1$ types, a wide range of forms differing more or less strongly one from the other in a variety of characters have been secured in *Datura stramonium*.[1] The extra chromosomal material which is responsible for their peculiarities can be transmitted to only a part of their offspring and hence such forms cannot breed true. Pure-breeding types similar in appearance to some of the $2n + 1$ forms just mentioned have become possible, however, now that a knowledge has been gained of the effects of different parts of chromosomes when present as extras and now that a source of modified chromosomes with which to form new combinations has become available in our collection of prime types.[2] In the present paper we shall describe some of the methods of synthesizing pure-breeding types with extra chromosomal material without recourse to lethal factors.[3]

For convenience the 1·2 or largest chromosome was first chosen as source of extra material in attempting to work out methods of synthesizing pure-breeding types. The effects of this chromosome as an extra has been discussed elsewhere.[1] The primary $2n + 1{\cdot}2$ type called "Rolled" has two secondaries, "Polycarpic" ($2n + 1{\cdot}1$) and "Sugarloaf" ($2n + 2{\cdot}2$). Striking differences have been found in the physiology of their pollen grains[4] as well as in the appearance of the plants. The $1n + 1{\cdot}1$ grains of Polycarpic fail to germinate; the $1n + 1{\cdot}2$ grains of Rolled germinate but the tubes burst in the style and so fail to function; the $1n + 2{\cdot}2$

grains germinate and develop a slow-growing group of tubes which may take part in fertilization when competition is reduced by the application of a limited amount of pollen. Buchholz's studies showed that neither the 1·1 nor the 1·2 chromosomes could be transmitted through the pollen as extras but that the 2·2 half should be thus transmitted. These predictions have been confirmed by breeding experiments.

In addition to the secondary chromosome 2·2, several of the primary chromosomes (11·12, 13·14, 15·16, 21·22) can be transmitted by the pollen as extra material under favorable conditions. It might be expected therefore that occasionally individuals would be found in which these extras had been brought into the zygote from both the pollen and egg cells and that they would breed true. Such tetrasomic $2n + 2$ types have been identified involving the 15·16 and the 21·22 chromosomes. Their occurrence is rare, not only because the transmission of extra chromosomes through the pollen is rare under the usual conditions of pollination but because the survival value is greatly lessened in plants with two extra chromosomes. It is probably for these reasons that we have not identified other $2n + 2$ types in offspring where they theoretically would be expected.

The $2n + (15{\cdot}16)_2$ and the $2n + (21{\cdot}22)_2$ types do not breed true as might have been expected. The breeding records may be given for types with the 15·16 chromosome extra. Out of 1668 offspring from selfing $2n + 15{\cdot}16$ plants, there were 362 trisomic individuals like their parent and 7 (0·4%) recorded as $2n + (15{\cdot}16)_2$ tetrasomics. One of the tetrasomics when selfed threw 20 normal diploids, and 52 with extra 15·16 material. Of the latter 36 were trisomics and 16 tetrasomics. In the disjunctions of the four 15·16 chromosomes, apparently a $2 + 2$ separation is not the invariable rule. Instead, a $1 + 3$ disjunction is frequent which gives rise to the $2n$ and $2n + 1$ classes. Zygotes with 3 and with 4 extra chromosomes which might be expected are probably not viable. In tetrasomics there is apparently lacking any check upon the types of disjunction to prevent losses of chromosomes and a consequent return to the normal $2n$ condition. Such a check is the necessity to the gametophyte of all the twelve chromosomes and of all their parts so far investigated. This has checked the appearance of deficiencies in normal $2n$ *Daturas*.

Tetrasomics involving the addition of two extra secondary chromosomes have not been identified. Out of 1281 offspring of $2n + 2{\cdot}2$ parents, there were 254 individuals of the $2n + 2{\cdot}2$ type. No $2n + (2{\cdot}2)_2$ types were recognized although they may have been represented by certain weak plants which died before reaching maturity. Four extra ·2 halves would probably be such a severe unbalance that it would prevent continued growth without special methods of culture. If a secondary tetrasomic $2n + (2{\cdot}2)_2$ type were found and brought to maturity, a peculiarity of secondary chromosomes would act, in addition to the factors discussed

above regarding primary tetrasomics, in preventing such a plant from forming the starting point of a pure breeding race with extra ·2 material. Secondary chromosomes most commonly unite by their ends to form "doughnuts" at reduction and thus go to the poles without regard to the other chromosomes.

Extra chromosomal material in the form of fragments should be easier to get through the pollen than secondary chromosomes since the unbalance is less. Several such fragment types are known with extra ·2 material in *Datura*. One, called "Loafoid," has a free fragment which consists of an outer part of the ·2 half. It is equal in size to about one quarter of the 2·2 chromosome. Loafoid plants were so named because they resemble the $2n + 2{\cdot}2$ type called Sugarloaf. The complex of characters behaves in inheritance as a dominant. Thus a heterozygous Loafoid parent threw 81 normals to 53 Loafoids in which the Sugarloaf characters were more or less strongly expressed. A homozygous Loafoid, shown by cytological investigation to have 2 fragments, was selfed and produced a progeny in which were recognized 11 normals, 53 "weak" Loafoids and 23 "strong" Loafoids. Weak and strong refer to the degree of expression of the Sugarloaf characters and not to the vigor of the plants. Judging from the appearance of the strong Loafoids, they probably included some with three fragments although they were not studied cytologically. A number of other fragment types have been gotten homozygous for the fragment but in all cases they throw a considerable number of normals in their offspring as does Loafoid.

Fragment types as well as $2n + 1$ types discussed earlier cannot breed true because the extra chromosomal material which they contain is not necessary to the process of reproduction. Success in the attempt to obtain pure-breeding types with extra chromosomal material has been won, however, by ioining the extra material to chromosomes which the plant cannot get along without. Three examples will be given in which the extra material has come from the ·2 half of the 1·2 chromosome.

1. In the preceding paper, a prime type (*PT* 6) was listed which is characterized by a free ·1 fragment and an attached ·2 portion forming the 2·11·12 chromosome. These ·1 and ·2 portions are of value in making up compensating types[1] and in synthesizing pure-breeding types as will be seen shortly. By selfing a parent heterozygous for *PT* 6, the ·1 fragment was eliminated and a type homozygous for the attached ·2 fragment was secured. It has been listed as *PT* 5 and its formula may be written $2n - (11{\cdot}12)_2 + (2{\cdot}11{\cdot}12)_2$. The ·2 half must be carried by both pollen and eggs because it is attached to the only 11·12 chromosomes possessed by the plant. Without this chromosome the gametophytes would perish. The race has bred true for 5 generations and resembles closely the secondary type, $2n + 2{\cdot}2$.

2. It was seen that if the portions into which the 1·2 chromosome broke in forming *PT* 6 were equivalent to the portions making up the halves of the 1·1 and the 2·2 chromosomes, it ought to be possible to compensate the 1·1 chromosome with 2·11·12 and the 2·2 chromosome with the ·1 fragment. The compensating type $2n - 1{\cdot}2 - 11{\cdot}12 + 2{\cdot}11{\cdot}12 + 1{\cdot}1$ which has been secured cannot transmit its 1·1 chromosome through the pollen. Since it cannot breed true it need not concern us further here. The compensation between the 2·2 secondary chromosome and the ·1 fragment is of more interest. The ·1 fragment cannot be transmitted through the pollen as an extra and the 2·2 chromosome can be thus transmitted only under special conditions. It was useless to attempt to combine the two chromosomes by using pollen of a $2n + {\cdot}1$ plant on a $2n + 2{\cdot}2$ female and the mathematical chances of the reciprocal cross producing a $2n + 2{\cdot}2 + {\cdot}1$ zygote were small even if such a highly unbalanced plant should be capable of reaching maturity. Another method, therefore, was employed in getting the two chromosomes together. A $2n + 2{\cdot}2$ female was crossed with *PT* 6. The $2n + 2{\cdot}2$ individuals in the progeny were heterozygous for the ·1 fragment and for the attached ·2. In the next generation a number of Sugarloaf types would be expected such as homozygous and heterozygous *PT* 5, the secondary $2n + 2{\cdot}2$ and types homozygous and heterozygous for the compensating chromosomes 2·2 and ·1. It was possible to eliminate the normals and the heterozygous individuals with weakly expressed Sugarloaf characters by inspection. Among the strong Sugarloaf individuals, one with about 15 per cent aborted pollen was chosen for cytological investigation since it was expected that the desired type would give a considerable proportion of aborted pollen. It was found as expected to have two 2·2 chromosomes and two ·1 fragments. Its formula may be written $2n - (1{\cdot}2)_2 + (2{\cdot}2)_2 + {\cdot}1_2$. It contains no 1·2 chromosome. The necessary 1·2 material is divided between the compensating chromosomes 2·2 and ·1. Each whole 2·2 chromosome is therefore necessary but each has an unnecessary ·2 half extra. The two 2·2 chromosomes tend to form "doughnuts" at metaphase and go at random to the two poles. Pollen grains which lack a 2·2 chromosome will abort, since no gametophyte with a deficiency is viable. By non-disjunction, zygotes with an extra 2·2 or with an extra ·1 chromosome might be expected. Such types would be highly unbalanced and would have difficulty in reaching maturity. If they lived to produce seed, their offspring would tend to revert to the type under discussion. They could never produce normals since the 1·2 chromosome is lacking. The type has been under observation for only 2 generations. It is indistinguishable in appearance from the $2n + 2{\cdot}2$ type and appears to breed true.

3. The third pure-breeding type was synthesized from three different

prime types. *PT*'s 9 and 10 were combined and crossed with *PT* 12. A plant with Sugarloaf appearance in the F_2 was identified cytologically as having the following composition: $2n - (13{\cdot}14)_2 - (23{\cdot}24)_2 + (2{\cdot}14)_2 + (\cdot 24)_2 + (13{\cdot}23)_2$. The plant entirely lacked the normal 13·14 and 23·24 chromosomes. The 2·14 chromosome from *PT* 10 compensated with the 13.23 chromosome of *PT* 12 to give the equivalent in chromosomal material of a 13·14 chromosome. The 13·23 chromosome also compensated with the ·24 fragment from *PT* 9 to give the equivalent of a 23·24 chromosome. There was left over after these compensations a ·2 half chromosome. Since the plant was homozygous for the modified chromosomes and had two normal 1·2 chromosomes, it had two extra doses of the ·2 half and in consequence showed the Sugarloaf characters of the $2n + 2{\cdot}2$ type. It has been cultivated for two generations. It appears to breed true, as would be expected since the ·2 half is joined to the ·14 fragment necessary to the life of the gametophytes. It is probable that in bringing in the compensating chromosomes ·24 and 13·23, we have brought in also extra material from the 23·24 chromosome, judging from certain added peculiarities characteristic of the $2n + 23{\cdot}24$ type.

Photographs of these three synthesized types are being published elsewhere.[5] In all three, extra ·2 material is present and induces similar morphological peculiarities in the appearance of the plants. The three are similar externally, and in the amount of chromosomal material in their cells. The distribution of this material in chromosomes however, is distinctly different. They are pure-breeding races and differ from the normal race from which they arose in a wide range of characters. Whether they are to be called new species in respect to the standard line depends upon the definition of a species. Morphologically they appear more worthy of the term than certain species of *Datura* already current in taxonomic literature.[6] Perhaps the chief respect in which they differ from described species in nature may be thought to be that we know their method of origin and have synthesized them according to previous specifications. It must be confessed, however, that no species in nature are known to have chromosome arrangements comparable to the three synthesized races which are here described. It must be admitted, on the other hand, that the chromosomal constitution of few species in nature have been adequately analysed and further study may show that shifting of blocks of genes and addition of extra chromosomal material may have played a greater rôle in nature than is now evident.

There are two prerequisites to the synthesis of pure breeding types with extra chromosomal material. (*a*) The extra material must be capable of being transmitted through the pollen as well as through the egg cells in order to obtain homozygous individuals. (*b*) The extra material must be joined to some chromosome or chromosomal part necessary to the

existence of the gametophytes in order to force the race to retain the unnecessary chromosomal material and hence to breed true. Since a number of primary, and at least one of the secondary, chromosomes are capable of being transmitted through the pollen, a considerable variety of

SUMMARY SHOWING TYPES IN DATURA WITH MODIFIED 1·2 CHROMOSOMES

The Secondary type $2n + [2 \cdot 2]$ has 25 chromosomes and cannot breed true.

The fragment type $2n + [2]_2$ has 26 chromosomes but does not breed true.

The type $2n - [11 \cdot 12]_2 + [2 \cdot 11 \cdot 12]_2$ has 24 chromosomes and breeds true.

The type $2n - [1 \cdot 2]_2 + \left\{ \begin{matrix} [2 \cdot 2]_2 \\ [1 \cdot]_2 \end{matrix} \right\}$ has 26 chromosomes and breeds true.

The type $2n - \left\{ \begin{matrix} [13 \cdot 14]_2 \\ [23 \cdot 24]_2 \end{matrix} \right\} + \left\{ \begin{matrix} [2 \cdot 14]_2 \; [\cdot 24]_2 \\ [13 \cdot 23]_2 \end{matrix} \right\}$ has 26 chromosomes and breeds true.

The type $2n - \left\{ \begin{matrix} [1 \cdot 2]_2 \\ [5 \cdot 6]_2 \\ [11 \cdot 12]_2 \end{matrix} \right\} + \left\{ \begin{matrix} [1 \cdot 5 \cdot 6]_2 \\ [2 \cdot 11 \cdot 12]_2 \end{matrix} \right\}$ which would have 22 chromosomes and breed true, might be synthesized if chromosome $[1 \cdot 5 \cdot 6]$ were available.

genes in chromosomal blocks is usable as extra material for the synthesis of pure-breeding races. If a chromosome cannot be carried by the pollen as an extra, this fact may not be evidence that one of its halves may not be transmitted. The 2·2 chromosome is poorly transmitted as an extra but the ·2 half alone or attached to form the 2·11·12 chromosome is

transmitted by the pollen with little hinderance because of the lessened unbalance which it exerts.

Success in tying usable extra chromosomal material to essential chromosomes or chromosomal parts is dependent upon having available an assortment of modified chromosomes upon which to draw. Such an assortment is available in a collection of prime types discussed in the preceding paper. The chromosomes formed by simple translocations like those in *PT* 6 are especially valuable. With the material available and with the methods already successfully employed it is evidently only a matter of time before it will be possible to synthesize a considerable number of pure breeding types with different kinds of extra chromosomal material and hence with different external characters.

The present paper is a contribution to methods. Their ultimate use in economic forms may depend upon first obtaining a knowledge of the effects of individual chromosomes and parts of chromosomes when present as extras.

The types discussed in the present paper are summarized in the adjoining table. It will be noted that one of the synthesized pure-breeders has 24 chromosomes, the same number as normal diploids, while the other two have 26 chromosomes. The last type in the table has not yet been synthesized since no case has yet been found among our prime types in which a ·1 fragment has been translocated to a normal chromosome such as the 5·6 chromosome suggested in the table. The hypothetical type would have only 22 chromosomes, or two less than the normal number. If no extra material were present it would be normal in appearance. From such a type, however, it should be possible to synthesize a 22 chromosome pure-breeding race with extra material by combining it with a prime type which had a pollen-transmissable fragment attached to another chromosome.

[1] Blakeslee, A. F., Smithsonian Report, 431–450 (1930).

[2] Preceding paper, these PROCEEDINGS, **19**, 103–115 (1933).

[3] Any secondary $2n + 1$ type could be forced to breed true, at least all its adult offspring would be like their parent, if it could be rendered duplex for a zygotic lethal whose allelomorph is located in the secondary chromosome, provided the lethal is incapable of crossing over. An approach to this condition has been found for the secondary $2n + 17{\cdot}17$. The gene curled (*c*) affects the cotyledons and reduces the viability of the seedling. It is in the ·17 half of the 17·18 chromosome but does not cross over. If it reduced the viability slightly further it would be called a lethal. In the offspring of secondary $2n + 17{\cdot}17$ plants with the formula $cc\frac{C}{C}$, all the *C* plants have been $2n + 17{\cdot}17$ secondaries and all the *c* individuals have been diploids, or the primary $2n + 17{\cdot}18$. If the recessive type had been albino, and the gene for albino did not cross over from the normal 17·18 to the 17·17 chromosome, a race would have been established which would produce only $2n + 17{\cdot}17$ adult offspring but which would always segregate for albinos among its seedlings. Lethals could be used in

similar fashion with tertiaries to give the effect of pure-breeding types if crossing over did not take place.

[4] Buchholz, J. T., and Blakeslee, A. F., these PROCEEDINGS, **16**, 190–195 (1930).

[5] Blakeslee, Albert F. In press, Proceedings of the Sixth International Congress of Genetics.

[6] *Datura tatula* differs from *D. stramonium* only by the dominant gene for purple in contrast to white flowers and *D. inermis* differs from *D. stramonium* by the recessive gene for spineless capsules. These forms seem no more worthy of specific rank than a number of gene mutations which have occurred spontaneously in our standard line of *D. stramonium* and seem better included in the latter species.

EVERSPORTING AS A FUNCTION OF THE Y-CHROMOSOME IN DROSOPHILA MELANOGASTER[1]

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Many eversporting characters have been encountered in plants and animals. Some cases seem best explained as unstable genes which mutate frequently (Emerson,[2] Demerec[3,4,5,6]). This paper describes cases of eversporting eye color in *Drosophila melanogaster* in which the incidence of sports is apparently dependent upon the distribution of an extra *Y*-chromosome.

Wild type males were treated with x-ray and mated to untreated females. Their first and second generation descendants were examined for sex-linked and dominant autosomal mutations. Three sex-linked mutations causing mottled eye color appeared, called mottled-1, mottled-2 and mottled-3.

Each of these mottled stocks produces, under certain conditions, red-eyed flies which are apparent reversions to wild type. Eversporting in mottled stock is not new. Muller[7] describes a mottled stock which segregates into dark and light mottled classes. He finds it possible to select darks which produce mostly dark progeny, and lights which produce mostly lights. Patterson[8] describes a different situation. He finds that red eyed flies from his mottled line produce the same proportion of mottled progeny as do their mottled sisters.

Our mottled stocks differ from each other in their amount of mottling. We have some evidence that an environmental agent, probably temperature, plays a large part in determining how much color is to be present in the eyes of mottled flies. Mottled-3, and to a less extent mottled-1, approach and actually overlap normal red eye color in their range of

variation. Breeding red eyed flies reveals that they fall into two classes: one comparable with Patterson's red eyed flies—merely normal overlaps which breed exactly like mottled flies; the other comparable with Muller's dark mottled class—a different genotype. This latter type of eversporting we have attributed to the *Y*-chromosome—a phenomenon hitherto undescribed.

The analysis of eversporting in mottled-2 will be presented first. Mottled-2 is linked with the *X* and fourth chromosomes. The *X*-chromosome is broken into two segments. The smaller segment contains the normal allelomorphs of yellow, white (?), facet and echinus, and is free. The larger *X* segment contains the rest of the *X*-chromosome including the normal allelomorph of ruby, and is attached to the fourth chromosome at its left or ruby end. Mottled-2 is semi-lethal to males, but when males do survive they are fertile. Homozygous females rarely survive and have not been found fertile as yet. By mottled-2 females, we mean females which are heterozygous for both *X* segments and for a normal *X* carrying white. The chromosome constitutions of mottled-2 males and females are represented by the following formula:

mottled-2 ♂ mottled-2 ♀

in which — means the small free *X* segment, ·—— means the larger *X* segment attached to a fourth chromosome, $\underline{\overset{w}{}}$— means a normal *X* carrying white, ⟶ means a *Y* and • means a normal fourth chromosome. The second and third chromosomes are normal and are not represented. All flies of the constitutions shown have mottled eyes. Our stock is kept by mating normal yellow, white, echinus, crossveinless, (*y*, *w*, *ec*, *cv*) males to mottled females whose normal *X*'s carry *y*, *w*, *ec*, *cv*. The progeny from such matings are white females, mottled females, and white males in about equal numbers, and a few mottled males. No hyperploid individuals are produced, and no red eyed nor haplo-IV progeny. Crossing over between mottled and *y*, *w* or *ec* has never occurred; *cv* crosses over less than 1 per cent. Thus it is evident that the broken *X*-chromosome in mottled-2 females behaves as an unbroken unit, its only abnormality being reduced crossing over. The case of mottled-2 males is very different. Separation of the two *X* segments, non-disjunction of the broken *X* and the *Y*, and non-disjunction of the fourth chromosomes, all occur very frequently, resulting in many hyperploid and non-disjunctional exceptions in addition to regular offspring. The exceptions of interest here are those which occur when non-disjunction of the broken *X* and the *Y* takes place. If such non-disjunction occurs in a mottled-2 male mated to a normal homozygous white female, the result is a red-eyed daughter of the constitution $\underline{\overset{w}{}}$ ⟶ (or a white-eyed *XO* son); if it occurs in a mottled-2 male

mated to a homozygous white attached-X female, ($\widehat{XXY}$), the result is a red eyed son of the constitution $\overline{\underline{\cdot:\cdot}}$, (or a white-eyed daughter with no Y). If bobbed is introduced into the mottled-2 and white stocks before making the former of the matings just described, the Y-chromosome can be followed by its inhibition of the expression of bobbed. That is, XO males and XX females look bobbed, but XY males and XXY females do not look bobbed. The red-eyed daughters from a mating of a mottled-2, *bb* male with a homozygous *w*, *bb* female do not look bobbed, but all their mottled sisters do look bobbed. When a red-eyed female $\left(\overline{\underline{\cdot:\cdot}}^{bb}\right)$, is mated to a *w*, *bb* male $\left(\underline{\underline{:}}^{w\ bb}\right)$ she has *w* $\left(\underline{\underline{:}}^{w\ bb}\right)$ sons; mottled $\left(\underline{\underline{:}}^{bb}\right)$ sons; *w*, *bb* $\left(\underline{\underline{:}}^{w\ bb}_{w\ bb}\right)$ daughters; *w*, not-*bb* $\left(\underline{\underline{:}}^{w\ bb}_{w\ bb}\right)$ daughters; mottled, *bb* $\left(\overline{\underline{\cdot:}}^{bb}\right)$ daughters; and red eyed, not-*bb* $\left(\overline{\underline{\cdot:}}^{bb}\right)$ daughters.

On cytological examination of oögonial divisions, mottled-2 females are found to have typical chromosome figures, but every figure from red-eyed females contains an extra chromosome, which looks like a Y.

Mottled-2 provides another example of the effect of the Y-chromosome on mottling of eye color. When mottled-2 males are mated to homozygous white $\widehat{XXY}$ females, many hyperploid daughters are produced of the constitution $\underline{\underline{\overset{w}{\underset{-}{>}}:}}$. Their eyes are dark mottled—distinctly mottled but very much darker than typical mottled-2. But occasionally a hyperploid daughter from such a mating has very light mottled eyes, even lighter than typical mottled-2. On the assumption that these represented $\underline{\underline{\overset{w}{\underset{-}{>}}:}}$ females which received no Y, due to non-disjunction of the X and Y in the father, one of these pale mottled hyperploid females was mated to a *w*, *B*, *bb* male. She had one *w*, *B*, *bb* son and he looked bobbed—proof that he received no Y from her.

The analysis of eversporting in mottled-3 is complicated by the fact that two distinct types of eversporting take place. Mottled-3 is linked with the X, second and third chromosomes. Males do not survive. Females are represented by the formula $\underline{\underline{\overset{\wedge\wedge}{w}}}\ \wedge\ \wedge$ in which $\overset{\wedge\wedge}{\underline{\underline{\quad}}}$ means the X, second and third chromosome complex responsible for mottling, $\underline{\underline{w}}$ means a normal X carrying white and $\wedge$ means a normal second or third chromosome. The fourth chromosomes are not involved. The symbol $\overset{\wedge\wedge}{\underline{\underline{\quad}}}$ is intended to represent only the fact of genetic linkage. No cytological evidence of attachment has been found.

A mottled-3 culture produces some females with mottled eyes and some with red eyes; we believe that all the mottled females are $\frac{w}{\quad}\frac{\wedge\wedge}{\wedge\ \wedge}$; some red eyed females are $\frac{w}{\quad}\frac{\wedge\wedge}{\wedge\wedge}$ and some are $\frac{w}{\rightarrow}\frac{\wedge\wedge}{\wedge\ \wedge}$. The data upon which this conclusion is based were obtained by mating mottled and red eyed females singly to *w*, *B*, *bb* males. Primary non-disjunction of the *X*-chromosomes occurs at a high rate in mottled-3 females, so that all such matings will produce *w*, *B*, *bb* males and not-*B* females in addition to the regular offspring expected of such matings. The *w*, *B*, *bb* males will look bobbed if they are primary exceptions from a $\frac{w}{\quad}\frac{\wedge\wedge}{\wedge\ \wedge}$ mother; they will look not-bobbed if they are secondary exceptions from a $\frac{w}{\rightarrow}\frac{\wedge\wedge}{\wedge\ \wedge}$ mother. All the *w*, *B*, *bb* sons of mottled mothers looked bobbed; some red-eyed mothers had *w*, *B*, *bb* sons which looked bobbed; other red eyed mothers had *w*, *B*, *bb* sons which looked not-bobbed. No not-*Bar* daughters from any type of mother had mottled eyes. All the mothers which produced *bobbed* sons also produced mottled daughters. The mothers which produced *not-bobbed w*, *B*, *bb* sons produced no mottled daughters. We interpret these data to mean that some of the eversporting in mottled-3 is a function of the *Y*-chromosome. The other type of eversporting in mottled-3 has a different explanation, possibly environmental as suggested earlier.

Eversporting in mottled-1 is also of two types, both rare. Mottled-1 is linked with the *X*, second and third chromosomes. Males of the constitution $\frac{\quad}{\rightarrow}\frac{\wedge\wedge}{\wedge\ \wedge}$ are fairly viable, sterile and have mottled eyes. Females of the constitution $\frac{w}{\quad}\frac{\wedge\wedge}{\wedge\ \wedge}$ have mottled eyes. Occasionally mottled-1 varies in its phenotypic expression far enough to overlap normal eye color. Non-disjunction has never been observed. Triploidy arose twice in mottled-1 stock. Mottled triploids $\left(\frac{w}{\quad}\frac{\wedge\wedge}{\wedge\ \wedge}\right)$, mated to *w* males, quite consistently produced mottled triploid and white diploid offspring and a few red-eyed diploid daughters. These red-eyed females, mated to white males, had white, red and mottled offspring. At the time these flies were in existence the function of the *Y*-chromosome in this respect had not been discovered. It now seems very probable that that type of eversporting may be analogous to eversporting in mottled-2 and mottled-3, due to an extra *Y*-chromosome.

In conclusion, we have attributed eversporting eye color in our mottled stocks to the well-known mechanism of non-disjunction of the *X* and *Y* chromosomes—primary non-disjunction being responsible for the initial appearance of sports; and secondary non-disjunction for their continued appearance in later generations.

A more detailed presentation of this work will appear in the near future.

[1] From the Rockefeller Institute for Medical Research, Department of Animal and Plant Pathology, Princeton, N. J.; and the Department of Biology, School of Hygiene and Public Health, Johns Hopkins University, Baltimore, Md.

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THE HIGHER CRYSTALLINE PLATEAU OF SOUTHEASTERN BRAZIL

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There has been considerable discussion concerning the relationship between the German concept of the "primärrumpf," and the American concept of the peneplain.[1] The word "primärrumpf" cannot easily be translated. It was introduced by Walther Penck to describe a surface of relatively slight relief which is maintaining or actually decreasing its relief in spite of continuous uplift. Penck's thesis challenges the interpretation of all high-level uniform surfaces as having resulted from baseleveling followed by uplift. He maintains that under certain conditions of accelerated uplift the headwater areas of a drainage system will not feel the effects of rejuvenation. While the larger, lower courses of a stream may be able to overcome the rise of the land and maintain or quickly reëstablish a graded condition, the upper parts of the stream system will not be able to do this. According to Penck a convex nick will be formed in the stream profile, bearing no relation to rock structure, and for a time the upper portion of the stream will be graded with reference to the top of this nick rather than to any general regional baselevel. In this way a high altitude surface is supposed to develop with actually decreasing local relief in spite of a constantly increasing altitude.

Such a high altitude surface of apparently decreasing relief exists in

the highlands of southeastern Brazil. Lying chiefly in southwestern Minas Geraes, north of the ranges of low mountains which form a rim to the highlands, and southwest of the Serra do Espinhaço of the central part of this state, is a plateau of crystalline rocks, drained by the Rio Grande, a tributary of the Alto Paraná.[2] Along the eastern border of this plateau, south of the Serra do Espinhaço, the general elevation of the interfluves is about 1200 meters above sea level. Excepting for this eastern rim, which corresponds quite closely to the divide between the headwaters of the Rio Grande and those of the much shorter streams flowing eastward directly to the Atlantic, most of the plateau lies between 1000 and 1100 meters. It is surmounted, however, by a few isolated conical peaks which rise some 400 meters above the general level.

The landforms of the plateau are strikingly subdued. The interfluves are flattish and broad; the valley sides graded and convex; the valley bottoms broad and swampy; the stream channels shallow and meandering. The very deep decomposition characteristic of the rainy tropics makes the surface exposure of solid bedrock very rare. On this mantle of unconsolidated material, soil creep is very active, and the feeble, overloaded headwater streams, not finding solid footing on bedrock even in their channel bottoms, are forced to wind ineffectually about in flat, marshy aggraded valleys. This would seem to fit quite well the description given by Penck of a "primärrumpf" which, in spite of its altitude, is at the moment decreasing in local relief.

The major features of the surface configuration of this part of Brazil result from quite recent faulting, and from the differential erosion of varied rock types. Under the tropical rainy conditions granites and gneisses decompose rapidly to great depths; but quartzites and schists remain much less affected by weathering. The great difference in resistance of these two groups of rocks is revealed by the sharp rise of the Serra do Espinhaço, composed of quartzites and schists, above the plateau we have just described, which is composed mostly of granites and gneisses. The isolated conical peaks, also, are composed of the more resistant rocks. As Branner,[3] and later Harder and Chamberlin[4] have pointed out, these resistant formations were infaulted into the granites at an early geologic period and exhumed by differential erosion: their steep sides, therefore, represent fault line scarps, probably obsequent.

In a recently published monograph on the geology of Minas Geraes, von Freyberg interprets the subdued landforms of the plateau as resulting from the accumulation of great masses of weathered material.[5] Regardless of any previous irregularity of the surface, this mass of regolith by sliding, flowing or creeping lowers and rounds the divides and chokes the valleys. Von Freyberg believes that such a process is a characteristic feature of lands in the rainy tropics.[6]

We may state the problem, then: was this 1000 to 1100 meter plateau given its uniformity of interfluve level solely by the foundering of deeply decomposed ridges and the filling and choking of the valleys in the area of granites and gneisses until, most of the slopes being graded, a uniformity of summit level was developed where none existed before; or has this foundering process only slightly modified and helped to maintain a pre-existing subdued surface produced near sea level by stream action and since uplifted?

The fact that the 1000 meter level is extended into the areas of quartzite and schist in mature valley bottoms does not furnish conclusive evidence for either of these alternatives. If the whole area were reduced to a peneplain by stream action, it is to be expected that while the relatively weak and decomposed granites and gneisses were being reduced to a late stage of peneplanation, the valleys in the much more resistant quartzites and schists would have developed no further than maturity. However, if a "primärrumpf" were developed at a high elevation on the weak granites and gneisses without any previous baseleveling, the streams descending from the higher areas of the Serra do Espinhaço would find that the newly established surface of accumulation on the plateau would act as a local baselevel below which they would be unable to cut.

There is another line of evidence, however, which seems to support the hypothesis of stream baseleveling. The crystalline plateau in eastern São Paulo state is covered by a series of stratified formations. Most of these are sedimentary, from Permian to Cretaceous in age; but included among them are the sills and flows of diabase so widespread in this part of South America. All these formations dip gently toward the west. The diabase, being more resistant than the sedimentaries, forms an east-facing cuesta; the sedimentary strata immediately in contact with the crystallines, being relatively weak, have been eroded to form a typical inner lowland. The crystalline plateau in northeastern São Paulo state reaches the edge of this inner lowland, which here becomes very narrow, at an elevation of 1000 meters; but toward the south, to the west of the ranges of mountains in southern Minas Geraes, warping brings the plateau level to about 800 meters. At this elevation it reaches the crest of the abrupt escarpment known as the Serra do Mar which terminates the plateau toward the sea. The important point is that in the north the 1000 meter level is repeated beyond the inner lowland by the summit level of the diabase cuesta; and in the south where the crystalline plateau lies at 800 meters, the top of the cuesta is also at 800 meters. Similar elevations, moreover, are reported by Maack from studies in the state of Paraná.[7] Such a widespread occurrence of the same levels on rocks of very different kinds seems to indicate a former effective operation of a regional baselevel, followed by uplift with warping and faulting.

The question remains, then, why that portion of this widespread peneplain in southwestern Minas Geraes should now, in spite of its elevated position, be decreasing in local relief. Von Freyberg's belief that this is the result of climatic conditions seems to be correct in part, but not the whole story. Those parts of the crystalline plateaus of southeastern Brazil which are drained by the shorter and more direct Atlantic drainage are now increasing in local relief in spite of identical climatic conditions. The position of the 1000 meter plateau at the headwaters of the Paraná system would seem to make possible the accumulation of weathered material—an accumulation which is not taking place in the areas drained by streams which are obedient to the regional baselevel.

Unfortunately for the testing of Penck's theory regarding the development of a nick in the profiles of streams in areas now being continuously uplifted, the nick which does occur in the Rio Alto Paraná and its tributary the Rio Grande is related to the passage of these streams over resistant rock. The lower course of the Paraná is graded with reference to its outlet near Buenos Aires. Along the eastern border of Paraguay, however, the Alto Parana flows through a narrow gorge, and on the northern border of Paraguay plunges over the Guayra Falls, held up by the resistant diabase. Above the Guayra Falls the Alto Paraná flows through a youthful but not very deep gorge, at many places interrupted by rapids. The lower part of the Rio Grande is also on diabase. Its profile is ungraded and quite steep as far upstream as the place where it first encounters the diabase, near the northeast corner of the state of São Paulo. Here we find the nick in its profile. Upstream from the diabase the slope of the profile is much less, the upper Rio Grande being virtually unaffected by rejuvenation. The nick at the edge of the resistant diabase forms a local baselevel quite independent of the regional one. The headwaters are aggraded because of the great quantities of load supplied to them. This area will continue to decrease in local relief until the Guayra Falls have worked headward beyond the diabase.

This interpretation includes a climatic condition favorable for the rapid weathering of the weak granites and gneisses; and a headwater position on a river interrupted in mid-course by a resistant rock formation. It does not seem to demand description in terms of a "primärrumpf," but only as another example of a peneplain modified by the specific conditions of structure, process and stage.

[1] W. Penck, *Die Morphologische Analyse*, Stuttgart, 176–177 (1924); W. Penck, "Die Piedmontflächen des südlichen Schwarzwaldes," *Zeit. Gesel. Erdk. Berlin*, 82–108 (1925); C. O. Sauer, "Land Forms in the Peninsular Range of California as Developed about Warner's Hot Springs and Mesa Grande," *Univ. Calif. Publ. in Geog.*, **3**, 199–290, esp. 212–213 (1929); W. M. Davis, "Piedmont Benchlands and Primärrümpfe," *Bull. Geol. Soc. Amer.*, **43**, 399–440.

[2] See map of surface configuration included as figure 3 in P. E. James, "The Coffee

Lands of Southeastern Brazil," *Geogr. Rev.*, **22**, 225–244 (1932). The author has in preparation a paper on the surface configuration of the area covered by this map, of which the higher crystalline plateau is the part discussed in this essay.

[3] J. C. Branner, "Outlines of the Geology of Brazil, to Accompany the Geologic Map of Brazil," *Bull. Geol. Soc. Amer.*, **30**, 189–338 (1919).

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[6] B. v. Freyberg, op. cit., pp. 284–285.

[7] R. Maack, "Urwald und Savanne im Landschaftsbild des Staates Paraná," *Zeit. Gesel. Erdk. Berlin*, 95–116, ref. on pp. 98–99 (1931).

STRUCTURE OF THE "ELLICOTT CITY GRANITE," MARYLAND

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Introduction.—The Ellicott City granite is situated four miles west-southwest of the city limits of Baltimore, Maryland. The Patapsco River valley furnishes good exposures across the entire length of the granite body. Investigations were begun as a demonstration in granite-tectonic methods and were carried on in detail, because of the special situation of this peculiar granite mass. The map, figure 1, comprises the granitic area and a part of the surrounding wall rocks and their structure.

The Problems.—The geologic map of Maryland and of Baltimore county shows a granite body which seems to be discordant within the Piedmont region, the strike of its long axis being NW-SE whereas the general strike of the region is NE-SW.

It is clearly seen on the map that the granite intruded the gabbro and the Wissahickon schist, where the latter formed a salient that penetrates far into the large gabbro complex.

This peculiar position of the granite raises a few questions:

The mode of emplacement of the granite.

The structure of the granite and its relation to the wall rock structure.

The structural position of the granite within the Piedmont.

Granite and gabbro } discordance or
Granite and Wissahickon schist } concordance?

Is the granite the top part of a hidden batholith?

The relation of the pegmatites to the system: Wissahickon schist, gabbro and granite.

The Rocks.—The rocks of the region are described in detail by E. B. Knopf and A. I. Jonas,[1] G. H. Williams,[2] H. Insley,[3] E. B. Mathews[4] and others. Several features are added here as they are of importance for the understanding of the structure.

The Ellicott City granite is considered to belong to the youngest series of intrusive rocks of the Piedmont region. It may be epi-Carboniferous.[5]

The granite shows a very distinct flow structure. Minerals and inclu-

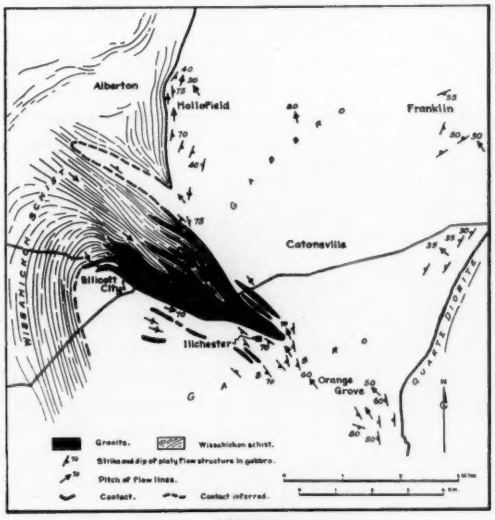

FIGURE 1

Map of the Ellicott City-Granite area and its adjacent wall rock.

sions are well oriented, see figures 2, 3 and 4. The flow structure can be seen under the microscope in oriented sections.

Inclusions within the granite are of special interest. Thousands of fragments of Wissahickin schist can be seen everywhere near the contacts. They can easily be determined on account of their structure and general aspect. Different from the schist are certain black inclusions within the neighborhood of Ellicott City (Weber Quarry). Knopf and Jonas[1] believe that they represent fragments of schist which are "almost swallowed up."

All the black inclusions show a very similar mineral composition. The gneiss or schist inclusions have their own structure preserved but it is not uniformly oriented parallel with the granite foliation. One can see

under the microscope in oriented sections, that the linear orientation within the black inclusions is, however, perfectly parallel to the flow lines of the granite. Therefore, the structure of the black inclusions is believed to be of the same age and origin as that of the granite. Although schist fragments are oriented parallel with the foliation of the granite since the foliation plane and cleavage plane are parallel by coincidence, it is doubtful whether the linear stretching in the schist would have to be parallel to the flow lines in the granite.

In view of the difference in the structural arrangements of the two groups of inclusions, the writer suggests that the black inclusions may be regarded as Autoliths rather than Xenoliths.[6]

The pegmatites are banded, especially near Illchester and Orange Grove. Fine grained layers change with very coarse ones. As the banding is always parallel to the dike contacts, the strike and dip of the pegmatites can be determined with accuracy. The best example of a banded pegmatite can be seen below the dam near Illchester. Most of the pegmatites form large dikes, which dip gently eastward at an angle of approximately 20–30°. Because their debris covers the slopes of the Patapsco river valley they appear to be larger and more numerous than they really are.

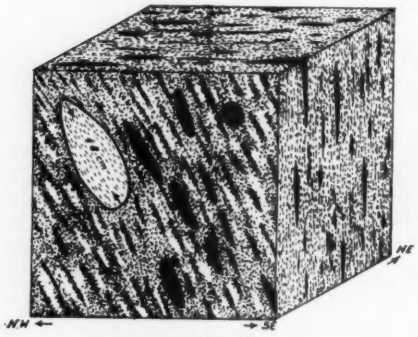

FIGURE 2

Schematic diagram of the structural elements in the granite (Weber quarry). Black: Autoliths of discoid shape indicating linear flow structure in their arrangement parallel to each other with their longest axis (front view).

The orientation of the pegmatites is closely connected with the structures of the granite and gabbro.

The gabbro (see Baltimore County rept., p. 107) is usually banded, and shows a very distinct linear flow structure. A detailed study of the gabbro structure has been begun by Charles Cohen at the Johns Hopkins University. The map shows strike and dip symbols for the gabbro only as far as is necessary for the understanding of the granite intrusion.

The Wissahickon schist forms the wall rock of the gabbro, granite and pegmatite. The schist represents the oldest rock within the above-mentioned group of rocks and the contact relations between it and the granite and gabbro are of special interest.

Structural Elements.—Structural elements in igneous rocks have been described so often in the literature, that the reader is expected to be ac-

quainted with them. For information see: Ernst Cloos,[7] Hans Cloos,[8] Robert Balk,[9] a. o.

The elements found in this region are the following:

A. *Linear Structures*
- *a.* Parallelism of needle-shaped crystals
  - Hornblende, titanite, epidote in the granite
  - Hornblende in the gabbro
- *b.* Parallelism of spindle-shaped inclusions
  - ? Autoliths in the granite
  - Xenoliths in granite and gabbro
- *c.* Chain-like swarms of inclusions of all kinds in granite and gabbro.

B. *Platy Structures*
- *a.* Minerals of discoid shape
  - Mica and feldspar in granite
- *b.* Inclusions of discoid shape
  - Autoliths and Xenoliths in granite
  - Xenoliths in gabbro
- *c.* "Banding" in gabbro
- *d.* Schlieren-like flexures in granite
- *e.* Dike-filled joints (pegmatite especially) in granite and gabbro
- *f.* Ordinary barren joints in granite and gabbro.

The elements in the granite are all primary, i.e., they originated within the stage of intrusion and consolidation of the magma. The layering in the gabbro is very likely primary and perhaps the linear stretching as well.

The above list of observable features is rather short compared with other regions of igneous rocks, e.g., the Sierra Nevada, California. In a previous paper[8] it has been shown that platy schlieren originate in response to differential flow in igneous rocks. Since schlieren are scarce in the present area, it would suggest that all parts of the magma except those near the contacts moved at approximately the same speed. Other considerations, about the shape of the space into which the granite was intruded, support this suggestion (see below).

The entire lack of schlieren combined with a large amount of Xenoliths and Autoliths suggests to the writer that schlieren are *not* always the remnants of assimilated inclusions, but the result of mineral accumulations by differential movements within the magma (see Hans Cloos). R. Balk has experiments in progress to demonstrate how movements within a magma can produce platy flow layers (schlieren).

Contact Relations.—1. Gabbro-Wissahickon schist.

The gabbro is intrusive into the Wissahickon schist and inclusions of schist in gabbro are abundant. They are oriented parallel to the gabbro banding and so assist in determining the direction of the flow structure. Discordant contacts are rare.

It is very striking that the salient of Wissahickon schist near Ellicott City was left more or less intact by the intruding gabbro (Fig. 1). The

salient is not broken up but the flow structure of the gabbro follows this irregular contact, changing its strike approximately 90°. The gabbro-schist contact is an old pregranitic surface along which the granite entered conformably as a new factor.

2. Granite-Wissahickon schist. The granite-schist contact is much more indented and irregular than the gabbro-schist contact. It resembles a lit-parlit injection on a large scale. (See Figs. 5 and 6.) Thousands of small granite tongues penetrate the schist, following its cleavage and bedding planes. Fragments are torn loose and can now be found as long leaf-like inclusions oriented parallel to the granitic flow structure. In mapping the area it is almost impossible to determine a distinct line for

FIGURE 3

Platy flow structure in granite, horizontal view, see top of figure 2.

the contact, because it is obscured through the increase of schist fragments outward from the center of the granite mass. The percentage of granite dikes decreases, and the proportion of schist increases accordingly, until finally the schist predominates. The Wissahickon schist salient is completely soaked with granite and broken into thousands of inclusions. Proceeding to the northwest, the schist gains ground, and gradually becomes the sole bedrock.

3. Granite-gabbro. The granite-gabbro contact is entirely different. It is extremely smooth and simple and a very well defined black and white contact with hardly any irregularities. Only a few dikes of granite were found within the gabbro (see Fig. 1). The ratio between granite dikes in schist and granite dikes in gabbro would probably be 10,000:1. The

contact follows the gabbro structure, but only because the gabbro structure follows the schist contact. The granite followed that contact, and respected the gabbro, because of its much greater resistance.

Internal Structure.—The flow structures of the granite and gabbro follow the contacts everywhere. Their strike and dip is therefore determined by the shape of the space into which the magma was intruded.

The gabbro and its structure will soon be described by Charles Cohen in a separate paper. A few of his results are mentioned here for better understanding of the granite structure.

The gabbro structure follows the schist salient, bending from a northeast-southwest direction into a northwest-southeast strike, or perpendicular to the general strike of the region. The dip of the flow structure points toward a central axis which runs from Franklin (see Fig. 1) through Catonsville toward Laurel, Md. The granite cuts across this axis at an angle of 90°.

FIGURE 4

Front view of figure 2, Weber quarry, Ellicott City. North left—South right.

The granite foliation strikes northwest southeast, with only one exception in the northwest corner of the area, where the body turns into the regional strike, paralleling the strike of the Wissahickon schist. The contacts of the granite are parallel to each other and dip almost vertical. The platy flow structure parallels the contacts and dips almost vertical also. Only the flow lines (linear structure) show an exception. They plunge toward the northwest within the southern part of the granite

body, and toward the southeast within the northwestern half of the body, thus indicating a center of intrusion approximately one mile southeast of Ellicott City.

Flow lines in the granite are parallel with the flow lines in the gabbro, both pointing toward the axial line mentioned before. It is very remarkable that the granite structure coincides with the gabbro structure. There are two explanations possible:

1. Flow lines in the gabbro and granite are of the same age. That would mean that the gabbro structure is a result of metamorphism at the time of granitic intrusion. In that case, the granite structure is primary and the gabbro structure secondary and superimposed.

FIGURE 5

Typical contact between granite and Wissahickon schist. Main Highway Ellicott City-Baltimore, 2 miles east of Ellicott City.

2. Both structures are primary and both magmas entered the present chamber more or less through "the same door," following a similar direction.

The first case seems unlikely, because the gabbro structure follows the contacts everywhere and it is unimaginable that regional metamorphism should produce a structure, which follows the irregular contacts of a certain limited mass so closely. Furthermore, if the granite intrusion is connected with the metamorphism of the gabbro, it ought to be strongest near the granite, but that is not the case.

The writer believes that the granite and gabbro intruded through the same gap. The gabbro intrusion followed the mentioned axis and widened upward. The granite broke through where the axis is crossed by the

granite body. The very gap is indicated by the flow lines in the granite.

Tension joints normal to the flow lines can be seen frequently wherever the flow lines are distinct. They are partly filled with pegmatites, e.g., near Illchester and Orange Grove. These pegmatites strike north-south and dip gently east. They are perpendicular to the linear stretching in the gabbro and the flow lines in the granite.

The pegmatite intrusion followed the granite closely, the interval between the formation of joints in gabbro and their vein filling must be greater than in the granite.

The Author's Interpretation.—The *gabbro* forms a wedge-shaped body, which narrows downward. It has been intruded *between* a number of gneiss domes which surround the gabbro today on all sides (see E. B. Mathews[10] and Baltimore County map[1]). The axis of this gap crosses the Patapsco river approximately one mile southeast of Ellicott City. A salient of Wissahickon schist was left intact by the gabbro, indicating a rather mild intrusive force of the magma.

The *granite* intruded into the weakest spot of the gabbro-schist system,

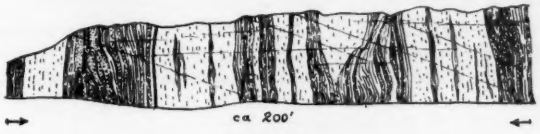

FIGURE 6

Section through the Granite-Wissahickon schist contact. Old Frederick road, east of Ellicott City.

namely, near the point where the schist salient crosses the axis of the gabbro body. The gabbro-schist boundary was used wherever possible but not sufficient space could be gained that way. We cannot assume that the small granite intrusion had the necessary force to push apart the very resistant gabbro blocks on each side along steep contacts. The only way out was *upward*, partly at the expense of the weaker Wissahickon schist. The latter was penetrated very thoroughly as the contact relation shows (see Figs. 1, 5 and 6.). A large amount of broken-up schist material was carried away, especially above the center of intrusion. The writer believes, therefore, that the space now occupied by granite was previously filled with schist. The granite intrusion began along the schist-gabbro contact and continued and widened during the process. Hardly any inclusions of Wissahickon schist are found above the focus of intrusion. The further we proceed to the northwest, away from it, the larger the percentage of unbroken schist until finally, several miles northwest from the main granite body the bedrock is Wissahickon schist exclusively. The gabbro blocks on either side of the granite remained unbroken and untouched.

The writer believes therefore that the granite body of Ellicott City is not the head of a larger batholith, which eats its way up into the crust at any place, but that we deal with "*selective intrusion*," for it has picked out the weakest spot available, beginning along petrographic boundaries, and widening the gap slightly by carrying away the flexible and strongly schistose material. Similar observations have been made in many other localities where batholithic intrusions were found on stratigraphic or tectonic boundaries (see H. Cloos, Riesengebirge[11]). The space which the granite occupies today was undoubtedly the easiest to get into and the only one which the granite could occupy without too much effort. The intrusive force seems to have been halted completely by the gabbro, but remained very effective within the Wissahickon schist. Further away from the main canal, the force died out rapidly and was not effective enough to disturb the schist seriously.

The different intrusive force of the gabbro and granite might very well result from the fact that the gabbro intruded into a space which widened upward, enlarging its horizontal surface constantly, but the granite was squeeezd into a narrow steep canal of constant cross-section.

[1] Knopf, E. B., and Jonas, A. I., *Maryland Geological Survey, Baltimore County*, The Johns Hopkins Press, Baltimore, Md. (1929); Knopf, E. B., and Jonas, A. I., "Stratigraphy of the Crystalline Schists of Pennsylvania and Maryland," *Am. J. Sci.*, **5** (1923); Jonas, A. I., "Pre-Cambrian Rocks of the Western Piedmont of Maryland," *Bull. G. S. A.*, **35**, 355–365 (1924).

[2] Williams, G. H., "Gabbro and Associated Hornblende Rocks of Baltimore, Md.," *U. S. G. S. Bull.*, **28** (1886); "Non Feldspatic Intrusive Rocks of Maryland," *Am. Geol.*, **3** (1890); "Geology of Baltimore and its Vicinity. Crystalline Rocks. Guide Book of Baltimore," *Am. Inst. Min. Eng.* (1892); "Volcanic Rocks of South Mountain," *Am. J. Sci.*, 3rd ser., **44**, 482–496 (1892).

[3] Insley, H., *The Gabbros and Associated Intrusive Rocks of Harford County, Maryland*, Diss., The Johns Hopkins Press, Baltimore, Md., (1928).

[4] Mathews, E. B., "Correlation of Maryland and Pennsylvania Piedmont Formations," *Bull. G. S. A.*, **16** (1905); Mathews, E. B., and Miller, W. J., "Cockeyesville Marble," *Bull. G. S. A.*, **16**, 346–366 (1905).

[5] Baltimore county report p. 131.

[6] Pabst, Adolf, "Observations on Inclusions in the Granitic Area of the Sierra Nevada," *Univ. Calif. Publ.*, **17**, 10 (1928).

[7] Cloos, Ernst, "Der Sierra Nevada Pluton," *Geol. Rundschau*, **22**, No. 6, 372–384 (1931); "Structural Survey of the Granodiorite South of Mariposa, California," *Am. J. Sci.*, **23**, 289–304 (1932).

[8] Cloos, Hans, "Bau und Bewegung der Gebirge in Nordamerika, Skandinavien and Mitteleuropa," *Fortsch. Geol. Pal.*, **7**, No. 21, Berlin (1928).

[9] Balk, Robert, "Primary Structure of Granite Massifs," *Bull. G. S. A.*, **36**, 679–696 (1925); "Die primaere structur des Noritmassivs von Peakskill am Hudson, etc.," *Neues Jahrb. Min.*, etc., Beil. Bd. **52**, Abt. B., 249–303 (1927).

[10] Mathews, E. B., "Anticlinal Domes in the Piedmont of Maryland," *Johns Hopkins Circ.*, **7**, 27–34 (1907).

[11] Cloos, Hans, "Tektonische Behandlung magmatischer Erscheinungen I (Granittektonik). Das Riesengebirge in Schlesien," Berlin (1925).

XENOHELIX IN THE MARYLAND MIOCENE

BY LINCOLN DRYDEN

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Communicated December 2, 1932

The name Xenohelix was proposed by Mansfield[1] for certain spiral structures found in the St. Mary's formation (Miocene) of Maryland. The forms illustrated have an ideal shape like that of a large and heavy corkscrew. Though not explicitly so stated, the Xenohelix described would seem to represent a boring or root hole whose periphery had become so indurated that the whole structure could be removed from the surrounding sand or clay. The "core," or part within the periphery, is not described as indurated.

The writer has found somewhat similar structures in the Calvert formation of Calvert County, Maryland. The locality is near the base of the bluffs on Chesapeake Bay, from 50 to 100 yards north of Randle Cliffs, or approximately $1^3/_4$ miles south of the steamer pier at Chesapeake Beach. Access may be had by automobile to Randle Cliffs. Any considerable breeze from the eastern quadrants renders visiting the locality unpleasant, especially so at high tide.

The Calvert formation has been divided into two parts: Fairhaven diatomaceous earth below, and the Plum Point marls above. Along the cliffs in this vicinity, only, has the contact between these two members been observed. That the contact is an unconformable one is shown by (*a*) an irregular and extensively bored upper surface of the lower beds, and (*b*) rising of the contact to the south against the regional dip. Figure 1, taken one-quarter mile north of the Xenohelix locality, shows the contact. The firm clay below is beset with borings which were formerly filled with the loose sand from above, now washed out by waves of the Bay. A band of Ostrea percrassa, persistent for about one mile, lies a few inches above the contact.

The Xenohelix of the locality cited is a vertical spiral with a central "columella," cut into the clay, filled with sands from the bed above. The filling is generally not present, since exposure of the spiral permits rapid removal of the sand filling, and, in addition, often destroys part of the structure itself, leaving a seemingly isolated part of a spiral. Careful uncovering of complete forms, however, shows that all these have a direct connection with the contact, and that they are filled with what is unmistakably sand from above. Connection with the contact is of two kinds: (*a*) "simple," spiral starting at contact and extending vertically downward, usually from a minor depression in the contact; (*b*) connection as

shown in figure 3, where average dimensions are also given. Figure 2 shows two typical specimens. In the form to the right, the columella has been largely destroyed, but it is present in the lower part of the specimen to the left. In figure 2 it appears that the spiral may be either right- or left-handed. A moment's reflection, however, will make it clear that the amount of erosion may determine the "dip" of the spiral remnants. If a left-handed spiral be just uncovered, the whorls will dip to the right; if eroded beyond the columella, they will dip to the left. If the columella be preserved, as in figure 2, it is possible to see immediately which way the whorl is descending. All of the some half-dozen examples at this locality were found to be left-handed.

Megascopically the clay matrix can easily be distinguished from the sand filling and from the sand above. The clay is firm light olive bluish green in color. Fossils are scarce and fossil fragments are rare. The sand above and filling the spirals is olive green in color, and contains a zone of fossil fragments a few inches thick at the contact. These fragments are generally absent from the spiral fillings.

An analysis of the clay, overlying sand and spiral filling gives the following results:

MECHANICAL ANALYSIS

SIEVE, MM.	CLAY BELOW, %	SAND ABOVE, %	SAND FILLING, %
1		1.8	0.2
1/2		1.8	4.5
1/4	8.5	11.7	11.5
1/8	9.3	23.2	21.8
1/16	37.2	31.2	31.1
Pan	39.6	26.7	26.5

The similarity of mechanical composition of the sand above and spiral filling is evident.

HEAVY MINERAL ANALYSIS

	CLAY BELOW, %	SAND ABOVE, %	SAND FILLING, %
Zircon	56	32	45
Tourmaline		5	5
Staurolite	4	25	13
Sillimanite	3	5	6
Garnet	9	17	12
Epidote	18	10	8
Kyanite	1	4	4
Rutile	1	1	1
Chloritoid	3	1	2

In addition to the above minerals a few grains of corundum, zoisite, clinozoiste (?), brookite and anatase are present in the sand and filling. A count of 200 grains was made on each sample.[2]

FIGURE 1

Contact between upper and lower Calvert formation 400 yards north of Randle Cliffs, Md.

FIGURE 2

Two examples of Xenohelix near Randle Cliffs, Md.

The mineral suite of the clay is different in character, also, from that of the others, in that the grain size is much smaller, staurolite is pale in color, epidotes not "typical," kyanite in broken, rounded fragments and in other features apparent to the eye. None of the rarer species enumerated was present in the slide from the clay sample.

One other fact is worthy of mention: the upper surface of the clay, even in the hollows and reëntrants, has a "leached" border of lighter color some one-eighth to one-quarter inch thick. This border or rim is not present

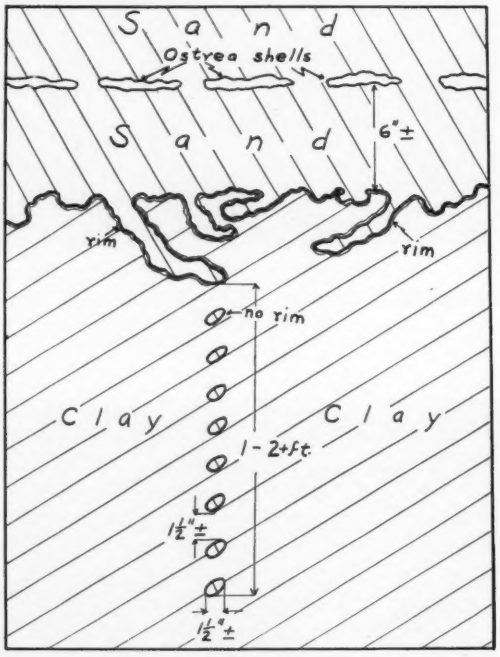

FIGURE 3

adjacent to the spiral itself. Though other explanations are possible, it seems probable that the spiral was made after the weathering or leaching had effected its work, since conditions are just as favorable for solutions to penetrate the spiral as the pits and hollows. Had the rim been post-dated Xenohelix the spiral should show it.

Origin of Xenohelix.—No definite proofs of the nature of Xenohelix have been adduced in this description. A summation of the facts as here found, however, limits the possibilities. It has been tacitly assumed that the structures are of organic origin.

(*a*). Xenohelix is a boring downward from a definite, unconformable surface and is always associated with that surface.

(*b*). The boring was made after the unconformable surface had been given its present configuration. Good, but not conclusive, evidence that subsequent erosion did not take place is found in (1) existence of weathering rim except where pierced by Xenohelix; (2) sharp change in mechanical and heavy mineral constitution across the contact, proving absence of reworking.

(*c*). Figure 2 suggests an animal rather than plant boring, particularly in the presence of a passage leading to the top of Xenohelix. Apparently the boring form had taken advantage of the passage already present, and on reaching the end of it had started the spiral structure.

(*d*). The absence of hard parts in the filling implies that hard parts were never present, i.e., that the borings were made by worms or similar soft-bodied forms.

(*e*). No reason is seen for associating irregular (non-spiral) borings with Xenohelix, as Mansfield has done.

Relation to Unconformities.—The relations of Xenohelix at this locality to the unconformity between the upper and lower Calvert formation is so marked that the possibility of such relationship, in general, obtrudes itself.

Mansfield's two described sections[3] in which Xenohelix occurs show that this form is found just under the Pleistocene contact, though there is some doubt expressed by that author as to just what is Pleistocene and what Miocene (St. Mary's).

In this same article, page 5, there is a reference to the occurrence of forms similar to Xenohelix in the uppermost layers of the fresh-water Molasse, just below the boundary of the marine Molasse. The upper beds have furnished the material of the spiral filling, as they have in Xenohelix of the Calvert formation.

Attention is called to this relationship to allow further verification, and also to facilitate the recognition of unconformities which might not be noticed except for the presence of Xenohelix or related forms.

[1] Mansfield, W. C., "Some Peculiar Fossil Forms from Maryland," *U. S. Nat. Mus. Proc.*, **71**, art. 16, 1–9 (1927).

[2] See A. L. Dryden, Jr., "Accuracy in Percentage Representation of Heavy Mineral Frequencies," *Proc. Nat. Acad. Sci.*, **17**, 233–238 (1931).

[3] Op. cit., p. 2.

CONFERENCE OF THE SYMBOLS, UNITS AND NOMENCLATURE (S. U. N.) COMMISSION OF THE INTERNATIONAL UNION OF PURE AND APPLIED PHYSICS (I. P. U.), AT PARIS, IN JULY, 1932, AND ITS RESULTS

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Communicated November 28, 1932

Preface.—This communication aims to present an unofficial summary of the actions, concerning C. G. S. Magnetic Units, taken by the S. U. N. Commission, at its Paris conference, July 9, 1932, together with a brief outline of the history of these units (since 1893) leading up to that conference, as well as a few deductions suggesting themselves therefrom.

Historical Outline.—Prior to the year 1893, the electric-circuit units *volt*, *ohm*, *ampere*, *coulomb*, *farad* and *quadrant* (later renamed the *henry*), had been internationally adopted to form a practical series. Similar action had been taken on the *joule* as a practical general unit of energy, and on the *watt* as a practical general unit of activity or power. All of these practical units were decimally related to the underlying centimeter-gram-second (C. G. S.) absolute system, and were in unitary or one-to-one relation among themselves. No units or unit names had, however, been adopted in the practical series for the magnetic circuit; although the Paris International Electrical Congress of 1889 had discussed practical magnetic units without taking action upon them.

At the International Electrical Congress of Chicago, in 1893, the question of adopting magnetic-circuit units in the practical series, was raised again. The Congress, however, in its Chamber of Delegates, recorded its decision in favor[1] of keeping these units in the C. G. S. System, and for the present, without names.

At the International Electrical Congress of Paris, in 1900, names[2] were suggested for four magnetic-circuit units in the C. G. S. System. After debate, it was voted to assign names to two units only: namely, the *maxwell* for the C. G. S. unit of flux Φ, and the *gauss* for the C. G. S. unit of magnetizing force H. There was accidental misunderstanding in the meeting as to the *gauss*. Some delegates believed and reported that it had been adopted for the C. G. S. unit of flux density B, until the official minutes showed that it had been assigned to H.

Suspension of Unit Making Functions by International Congresses.—There have been three international electrical congresses held since 1900; but none of them has taken action on electric or magnetic units. The Congress, of 1904, at St. Louis, recommended,[4] however, that inter-

national actions should be relegated, in future, to two commissions; namely, (1) International Conferences on Electrical Units, "representing the various governments, to consider questions relating to electrical units and standards upon which international agreement was desired." (2) The International Electrotechnical Commission (I. E. C.).

(1) Several successive International Conferences, composed of representatives from the various government laboratories entrusted with the maintenance of legal electrical standards, have been held since 1904, and have effected very important standardization among those units. They have not attempted to change existing units or unit names, or to add to them.

(2) The I. E. C., organized in 1906 by Col. R. E. Crompton, is a permanent body, with its General Secretariat in London. It comprises National Committees, in more than twenty countries, each representing various scientific and industrial interests. During its 26 years of activity, it has held 19 plenary meetings, distributed successively among 12 countries. Its principal work, divided among 18 Advisory Committees, has been standardization of machines and apparatus used in electrical applications; but important actions on the standardization of electric symbols, units and nomenclature, have been taken at different times, in its Advisory Committee No. 1, on Nomenclature. During the last seventeen years the I. E. C. has also authorized the convening of international electrical congresses.

Increasing Confusion in Magnetic Literature.—Since 1890 incipiently, and since 1900 definitely, there has been widespread ambiguity in the world's magnetic literature, over the definitions, names and symbols of certain magnetic-circuit units, and especially in regard to the *gauss*. No country has escaped this confusion completely. Some writers have used the *gauss* for the unit of magnetic flux density B exclusively, others for the unit of magnetizing force H, exclusively; and yet others for the units of both B and H indifferently. Moreover, some standard text books have taught that the quantities B and H are physically different and have different physical dimensions, under which condition, their ratio μ, the magnetic permeability of a medium, has also physical dimensions. In that case, the name *gauss* might apply to either B or H, but not to both. Other well recognized text books have taken the opposite position, i.e., that B and H represent physical quantities of the same nature, and of like dimensions, in which case their ratio μ must be dimensionless, or become a mere numeric, with the name *gauss* equally applicable to either unit quantity. It is therefore no wonder that there should be confusion and controversy as to the meaning and application of the *gauss*. No compromise was possible between these opposing points of view, and international agreement became necessary to smooth out the difficulty.

No action was taken until 1927, when the I. E. C., at its plenary meeting in Bellagio, Italy, considered certain proposals dealing with magnetic units. No international agreement being within sight during the discussion, the meeting appointed a special committee on Magnetic Units, representing seven countries, to consider the question and submit[5] a report.

Special Committee on Magnetic Units of I. E. C. in 1927.—This committee was unable to reach agreement, owing to the wide diversity of opinions presented; but reported in 1929 that[7] the question should be agitated in the various national committees and placed on the agenda for the next I. E. C. meeting (1930), in Scandinavia. In the interim, papers on the subject were read before electrical engineering societies and actively discussed.

I. E. C. Resolutions at Oslo in 1930.—When the special committee on Magnetic Units met in Scandinavia (June, 1930), its membership was increased to include twelve countries, and its name was changed to Section B of Advisory Committee No. 1 (Nomenclature), on Electric and Magnetic Magnitudes and Units (E. M. M. U).

It was found that, in order to reach agreement, it would first be necessary to arrive at a convention as to whether the quantities represented by B and H should be regarded as physically identical or physically distinct. After some discussion, the E. M. M. U. Committee agreed unanimously to recommend the convention that B and H should be taken as different physical quantities, and hence that their ratio μ, the "absolute permeability," should be regarded as a non-numeric. In vacuo, the ratio would be μ_0, the "space permeability" likewise dimensional. The "relative permeability" μ/μ_0 of a medium, would be thus taken as a dimensionless quantity, or a pure number.

The following unit names and units in the classical Maxwell C. G. S. Magnetic system were then recommended, either[8] unanimously or by a considerable majority: For the C. G. S. Unit of Magnetomotive Force F the name *gilbert;* Magnetizing Force H the name *oersted;* Magnetic Flux Φ the name *maxwell;* Magnetic Flux Density B the name *gauss*.

In this list, the *maxwell* had already been adopted at Paris in 1900. But the *gauss* assigned in Paris to H, was here selected for B. Moreover, in order to indicate that, in the opinion of the committee, the name *gauss* was not applicable to H, the name *oersted*, which had previously been used in America for the unit of reluctance R, without international support, was adopted for H.

The above recommendations, as well as others not dealing with C. G. S. units, and omitted here, were reported to the I. E. C. plenary meeting at Oslo, July, 1930, and were unanimously adopted.

S. U. N. Committee Appointed by the International Physical Union in

1931.—The International Union of Pure and Applied Physics (I. P. U.), meeting at Brussels in July, 1931, appointed[12] a new committee on Symbols, Units and Nomenclature (S. U. N.). The I. E. C. then requested the I. P. U. for the coöperation of the S. U. N. Commission with the E. M. M. U. Committee, on the questions involved in these magnetic units, and the S. U. N. Commission accepted the invitation.

Action of the E. M. M. U. Committee in London, September, 1931.—The above-mentioned I. E. C. resolutions on C. G. S. Magnetic Units, at Oslo in 1930, having given rise to certain criticisms in electro-technical journals, a meeting of the E. M. M. U. Committee, with a few members of the S. U. N. Committee in attendance, was held in London, to review the actions taken at Oslo, in the light of the criticisms that had been raised, and of the opinions reached thereon among the various national committees.

At the London meeting,[13] ten countries were represented. It was unanimously voted (two countries abstaining from voting), to endorse the I. E. C. actions taken at Oslo, in regard to C. G. S. Units.

Actions of the S. U. N. Commission Taken at Paris in July, 1932.—After sending out a questionnaire in December, 1931, on "Electric Units," to Physical Societies and physicists in different countries, in reference to the C. G. S. magnetic units, the S. U. N. Commission distributed a summary of the replies, and in view of the large number of physicists assembled in Paris for the International Electrical Congress, called an informal meeting for their discussion, at Paris, July 9, 1932. The meeting was held under the chairmanship of Sir Richard Glazebrook, Dr. E. Griffiths of the British National Physical Laboratory, being the Secretary.

The following propositions were adopted either unanimously, or by considerable majorities:

1. Any system of units recommended must retain the eight internationally recognized practical units: *Joule, Watt, Coulomb, Ampere, Ohm, Volt, Farad, Henry.*

2. The C. G. S. system of units is suitable for the physicist.

3. A system of practical units, including the above eight quantities, can be derived from these by multiplying the C. G. S. unit by appropriate powers of 10.

4. That M. Abraham, at the request of the conference, should prepare, for consideration by the Commission, a preliminary report on the Fundamental Units.

5. The system of magnetic units may be based on the following two methods as alternatives: (*a*) The force between two elementary magnet poles (Coulomb); (*b*) The force between two elements of current (Ampère).

6. *B* and *H* are quantities of different nature

7. The factor $4\pi/10$ should be retained in the definition of magnetomotive force.

The following table of electromagnetic quantities, which in accordance with suggestions received, has been revised since the meeting, is now proposed for adoption by the British representatives.

The S. U. N. Meeting then adjourned, after a vote of thanks of the chairman.

ELECTROMAGNETIC QUANTITIES

QUANTITY DESIGNATED	SYMBOL	C. G. S. UNITS EQUATION	C. G. S. UNITS NAME	VOLT-AMPERE UNITS UNIT	VOLT-AMPERE UNITS DEFINING UNITS
Flux	Φ	$\frac{d\Phi}{dt} = -e$	Maxwell	10^8 Maxwells	Volt-second
Induction or flux density	B	$\int B.dS = \Phi$	Gauss	10^8 Gauss	Volt-sec./cm.^{2}
Mmf. round a circuit	F	$F = 4\pi\, NI$	Gilbert or Oersted-cm.	$\frac{1}{10}$ Gilbert or $\frac{1}{4\pi}$ Ampere-turn	Amperes
Magnetising force or field strength	H	$\int B.\cos\epsilon.ds = F = 4\pi\, NI$	Oersted	$\frac{1}{10}$ Oersted or $\frac{1}{4\pi}$ Amp. turn per cm.	Amperes per cm.
Permeability	μ	$\mu = \frac{B}{H}$	Permeability	$\frac{10^9 \text{ Gauss}}{\text{Oersted}}$	$\frac{\text{Volt-sec./cm.}^2}{\frac{1}{4\pi} \text{ Amp. turn/cm.}}$

Comments Suggested on S. U. N. Commission's Actions at Paris Meeting.—An examination of the above propositions provisionally adopted at the S. U. N. Conference, shows that the Conference was opposed to any alteration of the classical C. G. S. system of units, by rationalization or otherwise. It also endorsed the I. E. C. Oslo convention that B and H are different physical quantities, by a vote of 9 to 3, 4 persons abstaining. From this the further convention follows, that absolute permeability μ has dimensions and is not a mere numeric. Moreover the S. U. N. table of units accepted in Appendix II, as given above, agrees in all essentials with that adopted at Oslo, so far as concerns C. G. S. magnetic units. Upon all essential C. G. S. questions, the S. U. N. recommendations appear to be in conformity with the I. E. C. recommendations of the E. M. M. U. Committee, at Oslo and at London.

If therefore, these joint I. E. C.-I. P. U. conventions are followed, the ambiguity and confusion of the past thirty years, in world magnetic literature of C. G. S. magnetic units, should disappear.

[1] *Proc. Internat. Elec. Cong. Chicago* (1893).

[2] *Congrès Internat. d'Electricité, Paris, Proces Verbaux* (1901).

[3] Report of Committee on Units at Paris, *Trans A.I.E.E.*, **17**, 552 (1900).

[4] Wolff, F. A., "The So-Called International Electrical Units," *Trans. Int. Elec. Cong. of St. Louis*, **1**, 143–169 (1904).

[5] "Rapport Général des Reunions tenues a Bellagio," Sept. *I.E.C. Fasicule*, **49**, 185 (1927).

[6] Kennelly, A. E., "Historical Outline of the Electrical Units," *Soc. for Prom. Engg. Education*, **19**, No. 3, 229–275, July (1928).

[7] Kennelly, A. E., "Magnetic Circuit Units," *Proc. A.I.E.E.*, **49**, No. 2, 486–510 April (1930).

[8] I.E.C., "Report of the Plenary Meeting at Oslo," July (1930); also I.E.C., Document R.M. 77, E.M.M.U. Meetings held in Stockholm, June-July (1930).

[9] Kennelly, A. E., "Units and Definitions Adopted by the 1930 Plenary Meeting of the I.E.C. in Scandinavia," *Elec. Engineering N. Y.*, **50**, No. 2, 141–142, Feb. (1931); also, *Revue Gén. de l'Electricité*, **28**, 722–725 Nov. 8 (1930).

[10] Mailloux, C. O., "La Question du Gauss," *Rev. Gén. de l'Elect.*, 125–135, Jan. 24 (1931).

[11] Kennelly, A. E., "Magnetic-Circuit Units Adopted by the I.E.C.," *Proc. A.I.E.E.*, Jan. (1931).

[12] Meeting of the International Union of Pure and Applied Physics, Brussels, July (1931).

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HIGHER PROCESSES IN THE BEHAVIOR OF RATS

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The experiments which I wish to describe briefly are concerned with what, I think, we must call reasoning in the rat. They involve giving adaptive reactions, where such reactions can come about only from combination, in advance of the reaction, of factors from separate experiences, and where such separate experiences involve essential contradictory or differing elements which must be functionally recognized. The first experiment is an extension, in terms of the enclosed maze, of the type of situation used by Maier in his study of reasoning in rats. The enclosed maze offers such different possibilities in the control of available cues, and has been so extensively used in other studies, that it seems desirable, for the sake of direct comparisons, to carry out such an experiment. The first form of this was conducted with Dr. Gardner Williams. The maze consisted of a central field (*C*), connected by independent alleys to each of four boxes. Each alley consisted of four or five sections, with a total length of eleven to seventeen feet, and laid out in a distinctive pattern. The boxes were of different shapes and contained various materials to

make them more distinguishable. All mazes in the study, unless otherwise stated, were built in the maze room which has no windows and is lighted by a system which can give no light cue.

The rats were allowed to explore the maze thoroughly, daily. Each day in the test, the animal was shown food in one of the boxes, made to explore the box, and then removed and placed in (*C*). He has run to every box several times during the day and found no food. He has now been shown food in one box, a different one each day. Will he be able to go directly to that box? Marked individual differences were found. I shall refer to some outstanding individuals by number. The first experiments with ten rats were during the fall term two years ago. Nos. 100 and 101 were among the most successful at that time, and nos. 93, 94 and 95 showed practically complete failure; nos. 92 and 97 were intermediate.

Then followed seven months of experiments in which the same rats were used in learning a variety of maze patterns; then a year ago, there were several months of additional work on reasoning, with the seven animals still alive.

In this second period, another 4-box pattern was used, but with each alley consisting of about twenty-five sections, with a total length of sixty feet or more. Also, instead of merely allowing the animal to explore the box, when food was shown, he was in each case run three or four times through the last few and characteristically patterned sections of alley, into the box where he found food. Nos. 93, 94 and 95 were again failures, the others successful, with 101 slightly the best. Nos. 93, 94 and 95 continued to fail even when they were run through nearly the whole length of the appropriate alley into the test box to find food, and then placed at (*C*).

New alleys were built from each box to a common food box (*B*). The rats were not allowed to invade these alleys during the exploration period each day. At the time of test, food was placed in (*B*), the gate removed between the appropriate box and new alley, and the rat was run through the explored box to (*B*), then placed at (*C*) to react. Only 101 continued a high grade record with this arrangement, though the records of 97 and 100 were probably better than chance. Adding distinguishing complexities in the explored boxes apparently bettered the performance of 100 and 97.

Two alleys from (*C*) were closed, thus reducing the available boxes to two, and the alleys connecting these two boxes with (*C*) were much shortened. No. 94 was now able to show success, but 93 and 95 still failed.

Shortened alleys were opened to three boxes during exploration. For the test, two alleys were closed and the rat run from (*C*), through the

third alley, to food in the chosen box. All three alleys were then opened and the rat placed at (*C*). All animals were now fairly successful, except that 95 showed a tendency to go first to the box that had been correct the day before.

Since 93 and 95 had thus far failed in all reasoning tests, they were given a long series in different two-box mazes. The first was built in an ordinary room, with one box near the window, the other box in the dark of the room. Both rats showed perfect performance. Shutters were closed over the window, and small, differentially located lights were placed over the alleys near each box. The lights were concealed from the central starting field. Both rats continued their success. Another maze was built in the maze room with its non-localizable lighting. Both rats showed better than chance results, but not very reliably so, especially in the case of 95. Lastly, another maze, built in the maze room, but with differentially located lights over alleys near each box, showed reliable success for both rats.

Someone will probably suggest that, in such a situation, the rat merely sets up a certain motor tension when run to food in one of the boxes, this tension depending upon the association of the specific box with the starting field (*C*), and being such as to govern the rat's movements appropriately when he is placed at (*C*). This suggestion is answered by a number of experiments, the clearest of which is as follows. A maze was constructed, containing three food boxes, and two starting fields, S_1 and S_2. For each box an alley ran from S_1 to join a similar alley from S_2, and from such junction a common alley led to the box. The responses required from S_1 were contradictory to those required from S_2. After the animal had been shown food in one of the boxes, he was placed sometimes at S_1; sometimes at S_2. After a successful response from one S, he was placed at the other. Nos. 92, 100 and 101 were used. No. 92 failed entirely while 100 and 101 gave almost perfect results. Such a result cannot be explained by a mere motor set.

The most striking experiment on reasoning is as follows. Suppose, in a maze with long, involved dead-end blinds, the end of one blind is placed next to a section of true path coming much later in the maze. After the animal has learned the maze to a high degree, the end of the blind is removed so that the former blind might constitute a short cut to the later true path. The animal is placed in the maze, passes the blind as usual, but pauses when he comes to the new opening. He explores a few inches into the former dead-end, and proceeds to the food-box. He is removed and placed at the starting point again. Success is shown by his ability to turn at the appropriate junction, through the former blind alley and direct to the food box. This problem is made much more difficult if a section of new path, hitherto unexplored, intervenes between the end

of the old blind and the true path section later in the maze. In a series of such tests, 100 and 101 showed nearly perfect results; and, in general, all rats showed substantially the same relative performance as in the other reasoning experiments.

It is of fundamental importance that, while the individual differences in all reasoning tests are quite uniform, there is apparently no relation between such differences and the ability to learn a maze with unique units; that is, a maze in which the patterns of alleys from junction to junction are all different. However, in other studies, we have shown that if a maze is used in which these patterns or units are all alike, and in which the reaction required at the end of all units is the same except that the last unit requires an opposite reaction, the rat cannot learn more than two or three units of such a maze except by the use of a cue from the floor as he runs over it, which cue is probably of auditory character. Now it is found that a few rats which can easily learn the unique unit maze are unable to learn the unit-alike maze. Among the rats which are able to learn the unit-alike maze, there is little relation, apparently, between the rapidity of such learning and the results with reasoning; but, so far, all rats that have been unable to learn the unit-alike maze have stood at the lower end of the scale in the reasoning experiments. This probably has to do with the delicacy of cues, but the problem is too complex for discussion here. One wonders what is the relation of all this to heredity, brain lesions and many other problems.

THE IN VITRO RESPIRATION OF NERVE

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We have previously reported that nerves kept in a medium containing a low calcium ion content show an increased respiration, similar to their heightened irritability. Even in the presence of adequate calcium, however, as in unbuffered Ringer solution, dog nerves (also brain, liver, kidney, muscle) at 37° show a marked rise in oxygen consumption after 6–7 hours (sooner in NaCl); whereas when suspended in dog serum such a late rise does not appear, at least for 20 hours. Further, at the start and until the rise begins, the absolute oxygen consumption in serum is greater than in Ringer (35 per cent for dog vagus: $Q_{O_2} = 174$ in Ringer, 237 in serum), due to other factors than calcium. Serum was handled in various ways in an attempt to identify the factors increasing the original

respiratory rate and preventing the late increase in oxygen usage. Despite results that spoke against a bacterial causation of the late rise, experiments under aseptic conditions finally proved bacteria to be responsible for it, the serum preventing their growth by moderately heat labile bacteristatic substances in the protein fraction. The initially high values in serum seem to be related in part to a similar fraction. Some of the facts established during the study are appended, and it may be noted that such respiration studies afford an admirable means of studying the antibacterial action of blood, as well as contributing information about the effect of blood constituents on tissue respiration.

The two effects of serum are not altered by preservation for 5 days at 5°C. Heating for 15 minutes at 80° or 1–2 hours (not half an hour) at 60° destroys the preserving action of serum but does not lessen its ability to increase the initial respiratory rate of nerve. Serum diluted with Ringer acts in proportion to its dilution in both respects. A protein-free ultrafiltrate of serum is not bacteristatic, nor does it increase nerve respiration to any extent above the value in Ringer. Cerebrospinal fluid behaves like the ultrafiltrate. Egg white acts much like whole serum in preventing bacterial growth and increasing nerve respiration, as does also serum after repeated ether extraction. The above evidence suggests the importance of proteins, but their action may depend on colloidal as well as chemical factors. Thus, gum arabic added to Ringer also delays considerably the bacterial rise in oxygen usage but lowers the initial rate. Nerves kept in Ringer, even if hypertonic, gain in weight over several hours, in some cases more than a third the initial weight, whereas in serum the gain is small (or absent). Heated serum (80°) again behaves like Ringer. Crude lecithin suspensions prevent the late rise and greatly depress the initial respiration, by half to three-fourths. Choline-free lecithin has little effect on the bacterial action but decreases the initial respiration, less than does lecithin itself; and acetyl choline greatly and progressively lowers nerve respiration to near cessation and prevents the bacterial rise. Of serum extractives, urea has no effect but the amino acid, glycine, added to Ringer or serum leads to a 20 per cent increase in initial respiration, without affecting the late rise. Lactic acid (contrary to the case of frog nerves at 20°) increases respiration; glucose does not. One-third of the creatine-phosphate of frog nerve kept in Ringer at 37° breaks down in three hours, one-half in nine hours. A nerve killed by boiling or grinding is attacked by bacteria much earlier than one not so treated.

OBSERVATIONS ON THE NERVOUS CONTROL OF RESPIRATORY MOVEMENTS

By Robert Gesell and Carl Moyer

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Studies were made on the anaesthetized dog under a variety of conditions to analyze the interplay of mechanical, chemical, central and peripheral influences controlling the respiratory act. Changes in circumference of the body were simultaneously recorded at three costal and four abdominal levels along with changes in tidal air, lung volume, mean blood pressure, heart rate and time.

Using the older method of classification of costal and abdominal breathing, the abdominal type was found in 60% and the costal type in 40% in 67 animals studied. Correcting for the greater displacement of air associated with unit change in circumference of the chest it was found that 60% of the animals now showed the costal type of breathing.

Many conditions were found to modify the type of breathing prevailing in any given animal. Prolonged experimentation with its usual increase in pulmonary ventilation, resulted in an increase in costal type of breathing from 60 to 80%. Administration of carbon dioxide and low oxygen mixtures, intravenous injection of sodium cyanide, sodium sulphide, sodium bicarbonate and sodium carbonate, mechanical asphyxias of various types, pneumo-thorax closed and open, nerve section and nerve stimulation produced characteristic effects upon costal and abdominal position and excursion and respiratory rhythm.

Mechanical asphyxia at the end of inspiration when the lungs are filled, was associated with markedly increased pulmonary pressures and a retarded rate of breathing. Mechanical asphyxia at the end of expiration was accompanied by decreased pulmonary pressures and, not infrequently, a retarded rate of breathing. Inspiratory mechanical asphyxia in which the animal is allowed to expire, but not inspire, was frequently accompanied by a large decrease in pulmonary pressures and volumes and not infrequently by a decreased respiratory rhythm. These results are in contrast to our findings on the same animals that respiratory rate is inversely proportional to pulmonary pressure if ventilation is allowed. Open pneumo-thorax in which the lungs are collapsed and immobile was associated with accelerated respiratory rhythm. Closed pneumo-thorax in which the chest opening is closed after collapse of the lungs, was associated with small excursions of the lungs and a further acceleration of the rate. Increased pulmonary pressure during closed pneumo-thorax which is unaccompanied by the usual increase in lung volume above normal

was associated with a super-normal respiratory rhythm. Carbon dioxide, low oxygen, sodium cyanide, sodium sulphide and sodium bicarbonate which under usual conditions exert an accelerating effect on respiratory rhythm had retarding effects during pneumothorax open and closed. Sodium carbonate which normally retards the rate exerted an accelerating effect during pneumo-thorax.

To summarize in a very general way our experiments emphasize the interplay of many influences, mechanical, chemical and nervous, controlling the rate, amplitude and coördination of respiratory movements.

ON THE METABOLISM OF THE PANCREAS

BY EUGENE U. STILL

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There are numerous problems of general interest concerning the mechanism of the secretion of pancreatic juice. This gland may be stimulated to activity by hormonal means without causing an important change in the rate of blood flow through the organ. The pancreatic juice is not only rich in organic solids and certain minerals but expecially so in bicarbonate. The bicarbonate content of the juice may be as much as seven times that found in the arterial blood. Before undertaking a study of the sources of constituents of the secretion and the mechanisms and conditions of their eliminations into the ducts, we have endeavored to determine under the most physiological conditions possible the respiration of the resting and active gland.

Our experiments have been on dogs under barbital anesthesia. The duodenum and pancreas were exposed. All branches of the pancreatico-duodenal vein were ligated except those draining the pancreas itself. This vein drains approximately one-half of the pancreas. Since there is little or no anastimosis between the drainage of the head and tail portions of the pancreas in the dog, we have measured the blood flow through the pancreatico-duodenal vein and assumed it to represent 50% of the total blood flow of the gland. We have assumed that 50% of the juice collected from the duct of Santorini was secreted by the half of the gland being studied. Further, we have assumed that the juice secreted by different parts of the gland was of the same composition with respect to the bicarbonate content.

An accurate electro-mechanical stromuhr which we have developed was inserted into the pancreatico-duodenal vein. Thus the vasomotor nerves

were left intact. The operation required that circulation be stopped for not over three minutes. Heparin was administered by a constant injection apparatus into the femoral vein to prevent coagulation of the blood in the stromuhr. The temperature of the animal was maintained, when necessary, by means of an electric animal warmer. The pancreatic juice was collected under oil. There were automatically recorded the following: blood pressure, rate of blood flow, rate of pancreatic secretion. After a period of from thirty to sixty minutes (to permit the pancreas to recover from the short period of asphyxia) the experiment was begun. Samples of blood for analyses were drawn from the femoral artery and from the tube

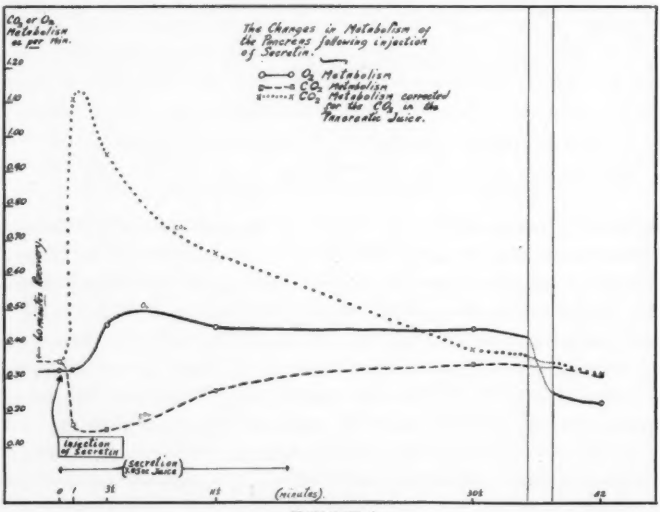
The Changes in Metabolism of the Pancreas following injection of Secretin.
O2 Metabolism
CO2 Metabolism
CO2 Metabolism corrected for the CO2 in the Pancreatic Juice.
Injection of Secretin
Secretion of Pancreatic Juice
(minutes).

FIGURE 1

entering the stromuhr (venous). The blood was preserved over mercury at 4°C. until analyzed.

Two or more samples each of arterial and venous blood were drawn as controls. Then secretin was injected into the femoral vein. Arterial and venous blood samples were drawn at intervals until complete recovery from the stimulation had taken place.

Results.—From the experiments we have found that the resting respiration of the gland is not constant but fluctuates between rather narrow limits. The oxygen consumption and carbon dioxide production may fluctuate singly or together. Although the rate of blood flow may be decreased by as much as 50% due to the withdrawal of blood samples, there was no appreciable effect upon the rate of respiration by the gland. The average resting respiratory quotient obtained by us was 0.87. The

minimum obtained was 0.71, and the maximum was 1.01. We believe the higher values indicate that the gland was not in a state of rest.

Figure 1 shows the changes in metabolism of the pancreas following the injection of secretin. The oxygen consumption rises rapidly during secretion and then slowly declines after the pancreas has ceased to secrete. The oxygen debt in some cases was as much as 50% of the extra oxygen used. The carbon dioxide content of the venous blood from the pancreas falls rapidly at the onset of secretion. This may be so marked that the venous blood contains but little more CO_2 than the arterial blood. In figure 1 the secretion of CO_2 in the juice was so rapid that the venous blood did not regain its resting CO_2 content during the period of secretion. If, however, one corrects the CO_2 metabolism curve for the CO_2 in the juice one finds that the CO_2 produced may be increased by as much as 300%. The extra oxygen consumption and extra carbon dioxide production from a short period of maximal activity as calculated from our data are about equal, indicating that the R. Q. during activity was 1.00.

It is of special interest that during secretion the arterial blood may contain 37 vol. % of CO_2 and the juice as much as 260 vol. %. Our data indicate that the metabolic CO_2 of the gland is diverted into the juice, rather than into the blood. We hope to have our data complete on this point in the near future.

I am indebted to Messrs. A. L. Bennett, V. B. Scott, B. G. Sarnat and Albert Hanke, all students, who have been associated with me in the conduct of these experiments.

PALEOZOIC PLANKTONIC FAUNAS OF NORTH AMERICA

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During many years of collecting graptolites there has been brought together a small assemblage of forms that are found associated with graptolites only in the typical graptolite shales. It consists of seaweeds, small sponges, cnidarians without skeletons (sea-anemones), inarticulate brachiopods with horny valves, a few small gastropods, worms and numerous crustaceans. On one hand none of the forms are found in any other rocks and on the other many of them possess a remarkably long time range and a wide areal distribution. The Graptoloidea or true graptolites are known to have led first a pseudoplanktonic existence, attached to seaweeds and finally a planktonic life by means of pneumatophores. It is to be inferred

also that the associated forms lived as pseudoplankton on floating seaweeds. The entire fauna exactly corresponds to the one living at present on the Sargassum fronds of the Sargasso sea, with the exception of the fishes that came later, and the abundant bryozoans, that are represented by the graptolites, probably an earlier branch of the class.

The distribution of the principal graptolite beds as well as their faunal composition indicate that these faunas that invaded the epicontinental seas originated in Sargasso seas that existed both east and west of North America in the Paleozoic Atlantic and Pacific Oceans or their respective ancestors. The presence of these Sargasso seas and the development of a well adapted fauna postulates as a corollary the early existence of these oceans, a view disputed by the adherents of the continental gliding theories.

A study of the distribution of the Paleozoic Sargasso-sea faunas shows that they were able regularly to enter only the large geosynclines paralleling the east and west coasts of America (Appalachian and Cordilleran geosynclines) and at long intervals the southern central basin from the Gulf of Mexico or Pacific and the northern margin (Greenland) from the Arctic ocean or North Atlantic.

A survey of the Paleozoic faunas of North America with a view to the discovery of further planktonic biota has afforded a number of sporadic occurrences of planktonic types in many formations, as Cambrian medusae and floating stocks of hydrozoans (Camptostroma); Ordovician and Devonian siphonophores (Discophyllum and Paropsonema), of which only the pneumatocysts are preserved; Cambrian to Devonian crustaceans with large swimming appendages, as in Marria, or crowns of spines to support them in floating as in Pephricaris. Most clearly adapted to a planktonic life were the larval stages of the trilobites either by accumulations of fat in the heads (glabella), as in Hydrocephalus, or by crowns of flat spines and marginal eyes, as in the anaprotaspis stage of Dalmanites socialis and many others. Also a number of full-grown trilobites were enabled to lead a planktonic or slow nektonic life at various levels of the sea by horizontal crowns of branching spines (species of Arges, Acidaspis, Radiaspis, etc.), or by possessing counter-balancing spines on the head to balance the body (as Lonchodomas) or on the body to counter-balance the head (as Ontarion). Some, as notably Aeglina had huge eyes, meeting on the underside and possibly also dorsal lighting organs (the "fossettes"), indicating that they floated in deeper waters.

A further survey of the Paleozoic formations of North America in regard to the possible planktonic origin of their faunas shows that most of the black shales (save the graptolite shales), while containing scattered planktonic elements, were formed in more or less enclosed basins and therefore contain only the remains of microscopic plant and animal plankton that is largely responsible for their carbon content, but is not indicative

of the open ocean as the source of the material as in the case of the Sargasso-sea faunas. Such is the Genessee shale which like the Genundewa limestone contains in the abundant Styliolinas a typical planktonic element, the Genundewa limestone representing a Devonian pteropod-ooze. The widely extending Chatanooga shale is characterized by the conodonts, now recognized as the teeth of cyclostomes. It was formed in near-shore and lagoonal areas where the cyclostomes died after the spawning season but which were not open to Sargasso-sea invasions from the ocean. The same is true of the Carboniferous and Permian shales.

It is probable that when attention is directed to the possible planktonic elements of the Paleozoic marine faunas, more forms will be recognized as being of that nature.

BIOLOGICAL INDUCTIONS FROM THE EVOLUTION OF THE PROBOSCIDEA[1]

BY HENRY FAIRFIELD OSBORN

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The extinct and living Proboscideans, including mastodonts and elephants of all the continents except Australia, of the 50,000,000 year period since Oligocene time in North Africa, have been intensively studied since the year 1907 or for the past quarter century for a monograph which will afford biological inductions even more significant than those set forth in Chapter X of the author's Titanothere Monograph of 1929.[2] Whereas the Titanotheres are geologically short-lived and variants of two chief types of adaptation, the Proboscideans are geologically long-lived, 55,000,000 to 65,000,000 years, and represent no less than fourteen widely distinct types of biomechanical adaptation to an environmental range from the Equator through the north and south tropics to the southern and northern continental extremities, guided by a surpassing intelligence, and guarded by tusk-like weapons equal or superior to any of those invented by man up to the introduction of firearms.

In brief, Proboscideans rank next to man in biological interest and far surpass man in confirmation of the principles of biomechanical evolution first set forth (Dec., 1931) in my seventh contribution to this series.[3] These six principles are: biomechanical evolution is (1) continuous or uniformitarian rather than mutational or cataclysmic, (2) germinal or centrifugal rather than somatic or centripetal, (3) creational in the Osborn sense rather than variational in the Darwin sense, (4) in geologic time

adaptively reactional rather than adaptively vitalistic or entelechistic, (5) syn-energistic and anti-energistic, that is, gathering energy to resist and overcome energy, (6) prior to somatic experience or prot-empirical, rather than after somatic experience or met-empirical.

The six principles above have slowly emerged during forty years of research, and are now confirmed by the Proboscidea. They act like lethal enzymes on the four chief historic hypotheses of the causes of biomechanical adaptation put forth in the twenty-five centuries since evolution was first conceived by the Greeks. These four hypotheses are: (1) adaptational use and disuse inheritance, as formulated by Lamarck. Lamarckism is moribund and unconfirmed (Osborn, 1929) by recent palaeontology. (2) As formulated by Buffon and St. Hilaire, environmental, physicochemical inheritance, through action on the germ, has been confirmed by field zoölogists and recently by experimentalists as a cause of germinal mutation and evolution in color and form. (3) Darwin's selection of favorable germinal variations camouflaged under a variety of terms now prevails among the zoölogists and the leading geneticists (e.g., Haldane, Morgan, Huxley) as the only indirect cause of adaptation which has been discovered. (4) Entelechy or internal perfecting tendency is not an explanation; it is a *petitio principi*.

Recent authorities (Haldane,[4] Morgan,[5] Huxley[6]) offer no new explanations, only variations of the old ones, enumerated above.

The twenty-five century problem of the origin of biomechanical adaptations remains unsolved by any of these four historic explanations. None of their modern substitutes conforms to the actual order or modes of evolution, derivable solely from paleontology, while wholly beyond the ken of zoölogy or experimentalism. When I say that there is not a scintilla of evidence for the adequacy of any of these four historic explanations as applied to biomechanical evolution I weigh my words carefully because I realize that I must be prepared not only to defend this statement but to substitute an entirely new concept of the complex of evolution phenomena which we sum up (Osborn, 1931) in the single word, *aristogenesis*.

Offsetting the temporary specific instability and inconstancy of the heredity-germ under physical and chemical experiment, paleontology demonstrates that the most fundamental principle is germinal stability; adaptive biomechanical change or variation of the germ-plasm is only secular. *Absolutely inevitable and germinally predetermined evolution, distinguished as aristogenic or always tending toward improvement, takes place in widely separated geographic areas, at the same or different evolutionary rates. The term aristogenesis applies to this germinal creative potentiality.*

Referring to my previous communications for details I now present to the Academy two concrete examples among many which are now demon-

strable in the evolution of the Proboscideans. They especially demonstrate three of the six principles above, namely: (1) *aristogenesis, the orderly creation of something better or more adaptive,* (2) *secular genetic reaction,* i.e., *creative origin from the germ plasm of entirely new germinal characters in the grinding teeth;* (3) *potential homogeny, the potentiality of the creative origin of new adaptive characters which distinguish certain lines of descent, the potentiality lying in a common germinal ancestry.*

The scene of the first example of proboscidean aristogenesis is from a descent line of mastodonts living in the Siwalik Hills of northern India during the flood plain deposition of 13,000 feet of Miocene sediment (Chinji 2300 feet; Kamlial 1700 feet; Murree 8000 feet; Gaj (Bugti) 1000 feet). The percentage of these Miocene strata to the whole Siwalik series of 16,000 feet is eighty-one. The time estimate of the Miocene period (Barrell, 1916) is from 12,000,000 to 14,000,000 years. We witness here the creative origin from the germ plasm in a definitely known period of geologic time of 24 new characters which may be tabulated as follows:

NEW ELEMENTS ADDED TO THE THIRD INFERIOR MOLARS IN THE PERIOD ESTIMATED AT 14,000,000 YEARS

		RIDGE CRESTS	CONES	CONELETS	CONULES	TREFOILS	TOTAL CONICAL ELEMENTS	TOTAL NEW ELEMENTS
Upper Miocene	*Trilophodon macrognathus*	5½	12	19	4	8	26	34
Middle Miocene	*Trilophodon chinjiensis*	5½	12	21	4	14	27	35
Lower Miocene	*Trilophodon palæindicus*	4½	10	17	3	6–7	20	27
Basal Miocene	*Trilophodon cooperi*	4⅙	10	17	2	0	19	19
Lower Oligocene	*Phiomia osborni*	3½	8	10	2	0	10	10

In the lower Oligocene *Phiomia osborni* the third inferior grinders, with the corresponding grinders above, condition the daily needs of crushing the requisite amount of herbage and are prophetic of the fact that in all Proboscideans it is the back molars on which biomechanical adaptation concentrates. Nine new elements are added in the Basal Miocene *Trilophodon cooperi;* seventeen new elements in *Trilophodon palæindicus;* twenty-five new elements in *Trilophodon chinjiensis;* twenty-four in *Trilophodon macrognathus.* Each of these elements rises from the creative potency of the germ, first as an inconspicuous rudiment, finally as a functional and useful cone or enamel folding. This phyletic series accordingly is a true picture of the evolution of the aristogenesis latent in the germ plasm.

The three principles of potential homogeny, of secular adaptive reaction, of the creation of something more adaptive, or aristogenesis, are absolutely and irrefutably demonstrated in these third inferior molars of a single line of descent. They conform with what has been repeatedly observed in other lines of descent. The fact that this creative aristogenesis is a totally unexplainable and mysterious process in no way invalidates or undermines this absolutely concrete and irrefutable evidence of the actual modes of the origin of new characters in species, genera and higher

divisions. These three principles are totally at variance with the working hypotheses of Darwin's variational-natural-selection, or of Lamarck's inheritance of acquired characters.

My second illustration is from the superior and inferior grinding teeth of the higher elephantoid division of the Proboscideans; it affords us a still more brilliant and convincing demonstration of the absence in biomechanical adaptation of anything in the nature of chance or experiment or trial and error. In the reciprocal mechanism of the grinders for the finer comminution of the food every mechanical adaptation of the upper grinders is reversed by an energetically counteracting adaptation in the lower grinders; the rates of these reciprocal upper and lower mechanical adjustments are precisely coördinated.

The enamel foldings by which the adaptive ridge crests rise from three in Oligocene time to thirty-seven in Pleistocene time constitute a potential characteristic of the Proboscideans. They begin with a low transverse ridge crest seen in a previous Miocene mastodont molar with a ganometric enamel length of 470 mm. (*Pentalophodon sivalensis*) which by multiplication of ridge crests and elevation of the enamel foldings rises to 6800 mm. in the highly complex mammoth stage of *Mammonteus primigenius compressus*. These are the extremes. In the closing Pliocene and entire Pleistocene of 1,250,000 years we are enabled by the new ganometric system[7] to demonstrate that each of the six great phyla or genera of elephants—*Archidiskodon, Parelephas, Mammonteus, Paleoloxodon, Loxodonta, Elephas*—has an independent line of grinding tooth evolution, progressive at distinct rates, slow, medium and rapid, parallel and similar but wholly independent. In fact, the end terms of this independent evolution produce grinding teeth so closely resembling each other that only recently has it been possible for Osborn to demonstrate that each of the six generic lines may be clearly distinguished when closely analyzed.

While fatal to Lamarckism in the temporary sense that all that is acquired is inherited, there is a vestige of the Lamarckian idea in the secular 14,000,000 year experience of the mastodont and elephantoid grinding teeth in that these new germinal characters and new germinal foldings do not rise spontaneously as they would on any entelechistic or vitalistic hypothesis. The twenty-six new conical elements or thirty-four total new elements observed in the mastodontoid series appear in secular response to the demands made on the feeding mechanism by different kinds of food. They are closely proportioned to the whole amount of feeding energy which is thrown upon the grinding teeth. Where other feeding organs, such as the incisive tusks, share the problem of the feeding animal as a whole the grinding tooth mechanism is much simplified. The same principle is observed in the contrast between the conservative grinding teeth of the modern African elephant which have remained in an upper

Pliocene stage of evolution with a ganometric scale of 2300 mm. while the grinders of the modern Indian elephant attain a length of 7850 mm.

Fatal as biomechanical evolution is to Lamarckism it is still more fatal to Darwin's working hypothesis of adaptation through survival of variations in any degree subject to chance. First, chance is absolutely eliminated both theoretically and actually by Proboscidean evolution; second, the rapidity of evolution is now known to be entirely independent of the rapidity of selection. In the Pleistocene million year period extremely slow-breeding elephantoids evolve their grinding teeth with amazing rapidity, far outstripping any of their rapidly breeding mammalian contemporaries in which it is difficult to distinguish a Lower Pleistocene specific stage from a modern specific stage.

The evolution of the Proboscidea undermines the inductions of the experimentalists and geneticists by demonstrating the non-significance of the larger portion of modern genetic discoveries. Only Bateson, founder of modern Genetics, had the courage to frankly throw up his hands in despair of obtaining really significant results as to the origin of species. The larger number of modern zoölogists are committing suicide by adopting a Darwinian creed, to use the elder Huxley's significant phrase. The attempt to trace the temporal origin of biomechanical adaptations, which paleontology demonstrates are *determinate, orthogenetic, secular, germinal processes involving enormous periods of time*, shows that the mutationists and selectionists are traversing a swamp of useless inquiry led by the will-of-the-wisp of expectation.

We must confess that biology is at present a totally uncoördinated science still in its infancy. It is not a science in the sense of astronomy or physics or chemistry. As compared with astronomy it is what astronomy would be if after the discovery of the spectroscope the whole structural astronomy had been abandoned. In other words, when we biologists abandon morphology, as the great majority are doing, we are leaving out of consideration the phenotypic aspects of heredity. Certainly no one could dream of the creative evolution of the germ plasm without the aid of the penetrating secular vision of modern vertebrate paleontology.

[1] This is the eighth contribution on the Origin of Species, and the principles of biomechanical evolution as demonstrated in vertebrate paleontology.

[2] "The Titanotheres of Ancient Wyoming, Dakota and Nebraska," Monograph 55, *U. S. Geological Survey*, Washington (1929).

[3] "New Concept of Evolution Based upon Researches on the Titanotheres and the Proboscideans," *Science*, Dec. 4, **74**, No. 1927, 557–559 (1931).

[4] J. B. S. Haldane, *The Causes of Evolution*, New York and London (1932).

[5] Thomas Hunt Morgan, *The Scientific Basis of Evolution*, New York (1932).

[6] Julian S. Huxley, *Problems of Relative Growth*, New York (1932).

[7] Henry Fairfield Osborn and Edwin H. Colbert, "The Elephant Enamel Method of Measuring Pleistocene Time. Also Stages in the Succession of Fossil Man and Stone Age Industries," *Proc. Amer. Phil. Soc.*, **70**, No. 2, 187–191 (1931).

THE TIME OF EMBRYONIC SEGREGATION IN APHIDS AS DETERMINED FROM INTERMEDIATE TYPES[1,2]

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Transplantation experiments by Spemann and many others have shown that the destinies of different parts of vertebrate embryos are fixed at different times in development. The same method is not readily open to students of invertebrate development, but it has been assumed that there is a similar succession of determinations in these groups. One important genetic theory, that of Goldschmidt concerning the nature of intersexes, includes the assumption that the embryonic segregations are serial in a definite order. Since intermediate forms may conceivably be produced without any time intervals between the determinations of their differential structures, it is desirable to discover whether such a succession of events does occur.

The crucial test of this serial segregation lies in obtaining intermediates by approach from opposite extremes. Such a test appears to be possible in aphids, in the forms intermediate between gamic and parthenogenetic females. The aphids have advantages for this purpose, in that they are all presumably alike genetically which is not true of the sexes, and that, since the intermediate form is induced by environmental means, there is a reasonable expectation that the intermediate stage may be arrived at from either the gamic or the parthenogenetic extreme.

The earliest intermediates between parthenogenetic and gamic aphids to be produced in numbers by experimental means were obtained by rearing winged females first at low, then at high temperature. Their early offspring were typical gamic females, the late ones parthenogenetic, with many intermediates in the transitional period.[3] Aside from the color of the body and the color of the antennae, both of which prove to be very variable, the changes observed in the offspring produced on successive days during the transition were as follows. The hind tibiae, which are much swollen in gamic females, became progressively thinner until they were indistinguishable from those of parthenogenetic females. During this thinning of the hind tibiae, the reproductive system was still strictly of the gamic form. Only in individuals in which the tibiae were already slender did the reproductive system show any modification, and the earliest offspring to exhibit such an internal change suffered a reduction or loss of the colleterial glands and seminal receptacle. Later offspring, in addition to lacking the colleterial glands and seminal receptacle, had their ovarioles changed in various ways and to different degrees toward the parthenogenetic type.

Complementary Types of Intermediates.—If the time-of-determination theory is applicable to those intermediates, the above facts would indicate that the ovarioles are determined or segregated first in the embryo, the colleterial glands and seminal receptacle next, and the hind tibiae last of the three structures. The proof of the applicability of the time-of-segregation theory lies in reversing the direction of change and obtaining intermediates of a composition complementary to that of the intermediates obtained in the first change. If aphids can be changed from parthenogenetic to gamic, and intermediates be obtained during the transition, the earliest intermediates should possess the differential structures which were lacking in the earliest intermediates obtained during the change from gamic to parthenogenetic. Since the latter had thin (or thinning) hind tibiae and a strictly gamic reproductive system, the former should have thick (or thickening) hind tibiae and a strictly parthenogenetic reproductive system. Intermediates a little later in the succession of offspring should have their colleterial glands affected. In the change from gamic to parthenogenetic, this change was a loss of the colleterial glands; and so, in the change from parthenogenetic to gamic the corresponding change would be the acquisition of colleterial glands, and the intermediate aphid would have swollen hind tibiae and colleterial glands, but wholly parthenogenetic ovarioles. Later in the succession of offspring the ovarioles would be changed; but while in the gamic-to-parthenogenetic transition the ovarioles would become parthenogenetic, in the reverse direction of change the ovarioles should become gamic. The structures should all change *in the same order*, but with respect to each structure the change would be *in the opposite direction* in the two directions of change.

Were the order of embryonic segregation rigidly maintained, no intermediate obtained by a change from parthenogenetic to gamic could be identical in structure with any intermediate produced during a change from gamic to parthenogenetic. Instead, they should be complements of each other. Early intermediates from one transition should possess the parts which early intermediates from the reverse transition lack; and the same should be true for later intermediates if individuals are taken from the same stage in the transition.

Absence of Complementaries in Early Experiments.—The reversal of the direction of change which, as just pointed out, constitutes the crucial test of the time-of-segregation theory was attempted in my former experiments,[3] but succeeded only in those cases where the parents whose offspring were being changed from parthenogenetic to gamic had previously been put from low temperature to high so that their offspring were changed from gamic to parthenogenetic. The two transitions in opposite directions were thus effected at different times in the lives of the same

parents. Intermediates were obtained during both transitions, but they were identical in their composition, not complements of one another. On its face, this evidence would contradict the theory that time of segregation enters into the production of intermediates. At least two other explanations were available, however, that were compatible with the time-of-segregation theory. These are discussed in my former article,[3] but one of them has since been rendered highly improbable.[4] The one remaining supposition which would permit one to adopt the time-of-determination theory is that the intermediates obtained in my former experiments were all *produced* during the first transition, but that some of them were not born until the second transition. The structure of the reproductive system is such that this delay in birth would be a physical possibility. Under these circumstances the two groups of intermediates should be identical, as they actually were.

Type of Evidence Sought.—What is needed to exclude this possibility is a transition from parthenogenetic to gamic in a family that commences purely parthenogenetic; that is, in one that has not already been changed from gamic to parthenogenetic. Preferably one or two generations of strictly parthenogenetic families should precede the change from parthenogenetic to gamic. The impossibility of making such a test immediately with the strain of aphids used in the former experiments is referred to in my earlier article, and more fully explained subsequently.[3,5] The facts are essentially these. For several years no family produced by winged parents of this strain had been exclusively parthenogenetic. There were always some gamic offspring, even when the parents were reared at high temperatures. At the risk of excluding winged offspring, which were of course necessary to the continuation of the experiments, the temperature at which the winged parents were reared was raised to 30°C., but even at this temperature, contrary to all previous experience, some gamic offspring produced. Since it was useless to attempt a transition from parthenogenetic to gamic in a family that was not parthenogenetic at the beginning, these efforts were discontinued.

The offspring of the winged parents which were reared at 30°C., were kept, as in all other experiments, at room temperature until they became mature. After the attempt to secure parthenogenetic families by high temperature was abandoned, it was observed that the last generation of their daughters produced yellow instead of green offspring (grandchildren of the last winged females reared at 30°C.), and that these grandchildren were nearly all winged, whereas the light conditions in which their parents were being reared should have made them mostly wingless.[6] The abundance of winged individuals, whatever its cause might have been, suggested an immediate repetition of the attempt to secure families that would begin wholly parthenogenetic, with the hope of changing them

to gamic later. Although high temperature was at first used to help induce parthenogenesis in the offspring, it was soon found that high temperature was unnecessary; the winged yellow females produced only parthenogenetic offspring at ordinary room temperatures. This condition appeared ideal for obtaining the transition to gamic offspring, and numerous winged females were promptly put at low temperature and various conditions of light, with the expectation that gamic offspring would appear late in their families, and intermediate ones during the change. Unfortunately, however, no gamic daughters were produced. The attempt was repeated many times, but without success.

In two generations, therefore, this strain of aphids had changed from a condition in which winged females could not be prevented from producing gamic daughters even by high temperature, to a condition in which they could not be induced to produce gamic offspring even by low temperature and alternating light and darkness.

Return of Gamic Females.—The new condition persisted for 13 months. During this time winged parents were repeatedly placed at low temperature, and one stock was kept continuously at low temperature; but always the offspring were exclusively parthenogenetic. The sudden modification of the behavior of the aphids, described above, occurred in November, 1929. It was not until December, 1930, that gamic females were again produced. At intervals since that time, the dates of which are roughly indicated by the last six headings of tables 1, 2 and 3, there have been moderate numbers of gamic females accompanied by intermediates. It is with the intermediates thus recently obtained that the present paper deals. Whether these intermediates were actually produced by a change from parthenogenetic to gamic is a question whose answer is best postponed until the aphids have been analyzed.

Analysis of the Intermediates.—Of the four hundred and more intermediates obtained in these experiments, those whose intermediacy lay only in the color of the body or of their antennae are not considered in this paper, owing to the apparently erratic variability of these colors. Attention is paid only to the three structural characters, (1) thickness of the hind tibiae, (2) the colleterial glands and seminal receptacle and (3) the form of the ovarioles. Also, all of the winged or partially winged gamic-parthenogenetic intermediates are omitted because of the demonstrated correlation[4] between wings and hind tibiae, such that possession of wings carries with it a thinning of the tibiae. There remain 288 intermediates to be analyzed.

If the earlier experiments[3] effecting a transition from gamic to parthenogenetic daughters, in which there were sharply defined relations among tibiae, colleterial glands and ovarioles, be relied upon to fix the order of embryonic segregation of these structures (assuming that there is a defi-

nite order), the change from gamic to parthenogenetic offspring may be divided into five recognizable stages. These are here stated as types of individuals which should appear in successive batches of offspring when the change is in the direction named. The gamic female has, of course, swollen hind tibiae, the gamic type of ovariole,[3] and colleterial glands and seminal receptacle. (Since the seminal receptacle is less easily recognized in dissections, and since its fate seems to be very closely bound up with that of the colleterial glands, the presence or absence of this group of accessory structures will henceforth be indicated by statements concerning only the colleterial glands.) The earliest offspring to show any change toward the parthenogenetic form had only partly swollen tibiae. This is indicated in the left nine columns of table 1 by placing the letter *x* in each of the appropriate columns. In the next recognizably more parthenogenetic offspring, the hind tibiae were slender, as indicated in stage 2 of table 1. After this character was completely transformed, the next step was a reduction of the colleterial glands (stage 3). A little later these glands had completely disappeared (stage 4). Then the ovarioles began to change to the parthenogenetic type. There are many features of this change, and they are indicated in stage 5 of the table by merely including both parthenogenetic and gamic ovarioles. Finally, with the conversion of all the ovarioles to the parthenogenetic kind, typical parthenogenetic females were produced.

TABLE 1

STAGES IN THE TRANSITION FROM GAMIC TO PARTHENOGENETIC OFFSPRING OF APHIDS AS INDICATED BY FORMER EXPERIMENTS, TOGETHER WITH THE REPRESENTATION OF THESE STAGES IN THE PRESENT GROUP OF INTERMEDIATES

	OVARIOLES		COLLETERIAL GLANDS			HIND TIBIAE			NUMBERS OF INTERMEDIATES IN DIVISIONS OF EXPERIMENTS					
STAGE	PARTH.	GAMIC	PRESENT	SMALL	ABSENT	SLENDER	PARTLY SWOLLEN	FULLY SWOLLEN	DEC., 1930	FEB., 1931	MAR., 1931	APR.-MAY, 1931	NOV., 1931	DEC., 1931
Gamic		x	x					x						
1		x	x				x		5	2	15	20	5	0
2		x	x			x			0	8	7	10	2	0
3		x		x		x			0	0	0	1	1	0
4		x			x	x			0	0	0	1	10	1
5	x	x			x	x			0	0	1	1	10	0
Parth.	x				x	x								

If, now, the nature of the intermediates depends on the time of embryonic segregation of their differential parts, the change from parthenogenetic to gamic offspring should be accomplished by the five stages indicated in the first nine columns of table 2. The hind tibiae should become partly, then fully, swollen; the colleterial glands should appear, at first slightly, then completely, developed; then some of the ovarioles

should change toward the gamic type. With the complete conversion of all ovarioles to the gamic type, the gamic female is established.

TABLE 2

STAGES WHICH MUST BE ASSUMED TO OCCUR IN THE TRANSITION FROM PARTHENOGENETIC TO GAMIC OFFSPRING, IN HARMONY WITH THE REVERSE CHANGE IN TABLE 1, IF THE SAME ORDER OF EMBRYONIC SEGREGATION OBTAINS, TOGETHER WITH THE REPRESENTATION OF THESE STAGES IN THE PRESENT EXPERIMENTS

STAGE	OVARIOLES		COLLETERIAL GLANDS			HIND TIBIAE			NUMBERS OF INTERMEDIATES IN DIVISIONS OF EXPERIMENTS					
	PARTH.	GAMIC	PRESENT	SMALL	ABSENT	SLENDER	PARTLY SWOLLEN	FULLY SWOLLEN	DEC., 1930	FEB., 1931	MAR., 1931	APR.-MAY, 1931	NOV., 1931	DEC., 1931
Parth.	x				x	x								
1	x				x		x		0	0	0	1	0	0
2	x				x			x	0	0	0	0	0	0
3	x			x				x	0	0	0	0	0	0
4	x		x					x	2	0	4	25	0	0
5	x	x	x					x	20	2	17	43	5	0
Gamic		x	x					x						

None of the five intermediate stages in table 2 is identical with any intermediate stage in table 1. It is possible, therefore, to classify intermediate females obtained in these experiments with reference to their composition, and thus to ascertain which, if either, of the transitions they fit. This has been done, and the numbers of the intermediates meeting the specifications of the ten intermediate stages are entered in the last six columns of tables 1 and 2. They have been divided according to the dates of their occurrence, in order that any progressive change in the frequency of any type might be detected. There is a total of 100 intermediates which conform to the scheme outlined for the change from gamic to parthenogenetic, and 119 that fall into the postulated series of parthenogenetic-to-gamic changes.

These two groups constitute more than three-fourths of all the intermediates under consideration. This large proportion probably indicates that the assumption that the composition of intermediates is determined by the times of embryonic segregation of their differential structures is, in a general way, correct. Were there no such relation between the structures, a much smaller proportion of intermediates should be of the kinds indicated in tables 1 and 2. Thus, since there are three distinguishable conditions with respect to each of the three structures, there are 27 conceivable types of individual. Two of these are the typical gamic and parthenogenetic females, the other 25 would be mosaics or intermediates. If the combinations were entered into at random, only two-fifths of them should be of the ten kinds listed in the two tables. Their actual numbers are nearly double this expectation.

One feature of the distribution of the regular or expected intermediates

(tables 1 and 2) which calls for comment is their accumulation near the gamic extreme in both transitions. The meaning of this is not clear. In harmony with the time-of-segregation hypothesis, accumulation of intermediates must probably be interpreted as due to a period of slow change, while few intermediates would be due to rapid change. In the present instance, the slow change is near the gamic extreme, but in one transition it involves change of the tibiae (table 1), in the other transition change of the ovarioles (table 2). The difficulty created by this situation is not any less if the threshold of stimulation be used to account for it. For accumulation of representatives in one stage of the process would presumably mean a wide gap between the threshold of beginning of a reaction and the threshold necessary for its completion, and in one of the transitions (table 1) the wide gap covers the range of stimulation of tibiae, and in the other (table 2) it covers the range of stimulation of the ovarioles.

Exceptional Intermediates.—Besides the 219 described above, there are 69 intermediates which do not fit either the gamic-to-parthenogenetic or the parthenogenetic-to-gamic transition. These are analyzed in table 3, where they are presented roughly in the order of their first appearance in the experiments. There are found to be twelve different kinds out of a possible fifteen.

TABLE 3

THE COMPOSITION OF INTERMEDIATES WHICH DO NOT CONFORM TO EITHER THE TRANSITION FROM PARTHENOGENETIC TO GAMIC OR THAT FROM GAMIC TO PARTHENOGENETIC

	OVARIOLES		COLLETERIAL GLANDS			HIND TIBIAE			NUMBERS OF INTERMEDIATES IN DIVISIONS OF EXPERIMENTS					
TYPE	PARTH.	GAMIC	PRESENT	SMALL	ABSENT	SLENDER	PARTLY SWOLLEN	FULLY SWOLLEN	DEC., 1930	FEB., 1931	MAR., 1931	APR.-MAY, 1931	NOV., 1931	DEC., 1931
1	x		x				x		7	0	5	2	2	0
2	x		x			x			4	0	0	3	0	0
3	x	x	x				x		3	0	4	5	0	0
4	x	x	x			x			1	0	4	14	0	0
5	x	x		x			x		0	1	0	0	0	0
6	x			x			x		0	0	3	0	0	0
7	x			x		x			0	0	1	0	0	0
8	x	x		x		x			0	0	1	0	0	0
9		x		x			x		0	0	0	1	2	0
10	x	x			x		x		0	0	0	1	0	0
11		x			x		x		0	0	0	0	3	1
12		x		x				x	0	0	0	0	1	0
	x	x		x				x	Possible but not found					
	x	x			x			x						
		x			x			x						

All of these exceptional types can be derived from the expected transi-

tional stages on the assumption that one or more of the three differential structures have had their fate fixed either earlier or later than the usual time. The simplest assumptions that can be made are listed in table 4, with the exceptional types which such assumptions would explain. The terms "early" and "late" in this table refer to time in a series of successive offspring during a period of transition, not to time of segregation which would be the reverse of this. When one change alone suffices to convert an expected type into an exceptional one, no other change is considered. All but one of the exceptional intermediates require but one change. Type 5 of table 3 requires two changes in time of segregation, but there are six ways of selecting the two. Some of the other exceptional types likewise can be derived in two or more equally simple ways, and these types appear more than once in the table.

It is quite possible that type 5, of which there was a only single individual, does not merit a separate category. It differs from type 3 only in that its colleterial glands are small. If it be supposed that these glands were diseased, or were reduced because of some other situation in no way connected with time of segregation, table 4 is somewhat simplified.

TABLE 4

CHANGES IN TIMES OF EMBRYONIC SEGREGATION NECESSARY TO PRODUCE THE EXCEPTIONAL INTERMEDIATES OF TABLE 3 FROM THE EXPECTED CLASSES OF TABLES 1 AND 2. ONLY THOSE INVOLVING THE SMALLEST NUMBER OF ORGANS ARE LISTED; OTHER DERIVATIONS ARE OBVIOUSLY POSSIBLE

POSTULATED CHANGES IN TIMES OF EVENTS IN SERIES OF SUCCESSIVE OFFSPRING	TYPES OF EXCEPTIONAL INTERMEDIATES
Late thickening of hind tibiae	1, 2, 3, 4, 6, 7
Late thinning of hind tibiae	9, 10, 11, 12
Late disappearance of colleterial glands	2, 4, 7, 8
Late production of colleterial glands	12
Early disappearance of colleterial glands	9, 11, 12
Early production of colleterial glands	1, 2, 6, 7
Early substitution of parthenogenetic for gamic ovarioles	1, 2, 3, 4, 8
Early substitution of gamic for parthenogenetic ovarioles	10, 11, 12
Late thickening of tibiae, *plus* early gamic ovarioles	5
Late thickening of tibiae, *plus* late appearance of colleterial glands	5
Late thinning of tibiae, *plus* early parthenogenetic ovarioles	5
Late thinning of tibiae, *plus* late disappearance of colleterial glands	5
Early appearance of colleterial glands, *plus* early gamic ovarioles	5
Early disappearance of colleterial glands, *plus* early parthenogenetic ovarioles	5

Of the remaining 11 exceptional types, ten *can* be explained by a change in the time of segregation of hind tibiae (first two lines of table 4). The remaining one, type 8 depends on a change in the time of segregation of either the colleterial glands or the ovarioles. Type 8 differs, however, from type 4 only in having small colleterial glands, and so, since there was

only one individual of that kind, it should perhaps be denied a separate classification, as may be justified for type 5.

There appears to be no way, however, of eliminating the remaining ten exceptional types. If, to make their explanation uniform, they all be regarded as due to a changed time of segregation of the hind tibiae (first two lines of table 4), to attempt to eliminate them would be to seek another explanation for the too-thick or too-thin tibiae. It has been shown[4] that there is a correlation between wings and tibiae, such that an aphid with swollen tibiae has them less swollen if it likewise possesses wings. But none of the exceptional intermediates here considered had wings; all winged or partially winged ones were omitted because of this known correlation. If it be assumed that the wing-producing agent might reduce the tibiae when present in too small an amount to produce wings, there are still left the intermediates in the second line of table 4, in which the hind tibiae are too large. Nothing in the experiments so far indicates any special explanation for these, hence it is probably necessary to assume that there actually is variation in the time at which embryonic segregation occurs. If this be true for tibiae, it may well be true for other structures, and the juggling just indulged in to reduce the exceptions to a single category may be quite unwarranted.

There is another possible source of the exceptional intermediates which, however, does not seem very probable. The transition taking place during the change from gamic to parthenogenetic offspring, or the reverse, no doubt involves a changing physiological level of some sort. The assumption is tacitly made in all the foregoing discussion that this change is a steady one. It may not be at the same rate at all times, but it is assumed to rise continuously or fall continuously over considerable periods of development. Goldschmidt has made this assumption in his explanation of intersexes, which involves successive embryonic segregations for the several differentiating structures, and a number of physiological processes are known to be represented by such curves. If, however, the level of the physiological process which determines parthenogenetic and gamic aphids is subject to sharp fluctuations in short periods of time, it is not necessary to suppose that the time of embryonic segregation of any organ fluctuates. For example, if this level "falls" early to, or starts at, a level which determines parthenogenetic ovarioles, then "rises" quickly to the level determines colleterial glands, and immediately "falls" in time to produce slender hind tibiae, an exceptional intermediate of type 2, table 3, results.

There remains the possibility that the threshold of stimulation of the several structures is different in different individuals. For example, if colleterial glands are in a given individual stimulated to development by an unusually "low" level, stage 5, table 1, may be converted into exceptional type 4, table 3.

Whether the situations described in the two preceding paragraphs are probable or not there is no present way of knowing; but they seem to be the only alternatives of the assumption that the time of embryonic segregation itself fluctuates frequently.

The Direction of Change.—It is not known from any independent evidence whether any of the intermediates described were produced during a change from parthenogenetic to gamic or the reverse. The doubt arises from the fact that it is uncertain how long a time the change requires. If it is a lengthy process, there are ways of determining its direction. Thus, after 13 months of strictly parthenogenetic reproduction, the first appearance of gamic forms would seem to mark a period of change from parthenogenetic to gamic tendencies. If experiments which were repeated at intervals of several weeks were to catch this change, the experimenter would have to be lucky or the change would have to take several weeks for completion. The nature of the very first few intermediates to appear after the long absence of gamic females is not entirely known, for they appeared during my absence from Ann Arbor and were not dissected while fresh. The presence or absence of colleterial glands could not be ascertained, but the aphids had swollen or partly swollen tibiae with ovarioles at least partly parthenogenetic, which would place them among the parthenogenetic-to-gamic intermediates of table 2. These intermediates are not included in any of the tables. In this instance the external evidence fits the evidence derived from analysis of the intermediates themselves.

The conditions under which the parents were reared do not offer positive evidence of the direction of change. In most of the experiments the parents were changed from room temperature to low temperature, which former experiments had indicated was favorable to gamic offspring. But some of the experiments involved a change of the parents from 14° to 24° and since gamic females and intermediates were obtained from both changes, the direction of change cannot safely be judged from the environmental conditions imposed.

More definite evidence of the direction of change would appear to be found in a limited number of the experiments in which successive offspring in the same families show a definite trend toward one type or the other. Six experiments have been selected in which there is a rather steady increase in the number of gamic offspring, and four others in which there is an even more striking decrease of gamic daughters. They are shown in table 5, in which intermediates are also included because they help to show the trend. Intermediates of both kinds occur in both groups. In each indicated direction of change there are more intermediates of the parthenogenetic-to-gamic types than of the gamic-to-parthenogenetic. Indeed, the surplus of the former is greater (second line of table 5) when

the trend indicated by the total offspring is in the opposite direction. Apparently the trend indicated by the family as a whole is no indication of the direction of change as it affects the individuals. A little better correspondence in table 5 could be obtained if it were assumed that the directions of change are exactly the reverse of those indicated in tables 1 and 2; but were that done, the very sharply defined results obtained from former experiments would stand in opposition.

TABLE 5

THE KINDS OF INTERMEDIATES PRODUCED IN FAMILIES SHOWING A MARKED TREND FROM PARTHENOGENETIC TO GAMIC OFFSPRING, CONTRASTED WITH THOSE SHOWING THE OPPOSITE TREND

TREND SHOWN	NUMBER OF GAMIC AND INTERMEDIATE OFFSPRING COMBINED IN FIRST 5 DAYS	IN SECOND 5 DAYS	IN THIRD 5 DAYS	NUMBER OF INTERMEDIATE OFFSPRING PARTH.-TO-GAMIC TYPES	GAMIC-TO-PARTH. TYPES
Parthenogenetic to gamic	25	90	175	29	18
Gamic to parthenogenetic	358	39	0	68	28

The most probable explanation is that the change of physiological level which affects the development of the individual is a very short-time process. It must also fluctuate considerably, in order that offspring developing in close succession may be of different compositions. Whether the fluctuations may be rapid enough to account for the exceptional intermediates without change in the time of embryonic segregation of any organ, is very doubtful. The author is inclined to the view that it cannot.

Summary.—If the nature of intermediates depends on the time of embryonic segregation of their several structures, those produced during a change in one direction cannot be identical with those produced during a change in the opposite direction. About three-fourths of the intermediate aphids here analyzed fall into the one or the other of these two mutually exclusive categories. Whether the direction of change was actually that which the composition of the intermediates requires cannot be ascertained from any other evidence. The external evidence as often indicates a direction contrary to, as in harmony with, that indicated by the nature of the intermediates. Nearly one-fourth of the intermediates do not agree with a postulated change in either direction. These exceptional forms may be attributed to (1) a frequent departure of the time of segregation of one or more structures from its usual stage of development, or (2) a sharp and rapid fluctuation, within the development of the individual, in the physiological level which constitutes the "turning-point" of determination, or (3) to differences in the threshold of stimulation of the several structures in different individuals. The author regards the first of these as the most probable, the second as least probable. In the two mutually exclusive classes of intermediates that agree with the time-

of-determination hypothesis, there is an accumulation of individuals near the gamic extreme. This may be interpreted as due either (1) to a slow rate of change, or (2) to a wide range of threshold of stimulation, near the gamic end of the series. These two interpretations face the same difficulty, in that in one direction of change it is the tibiae, in the other direction the ovarioles, which exhibit the slow rate of change or the wide range of threshold of stimulation.

[1] Contribution from the Zoölogical Laboratory of the University of Michigan.
[2] This work was aided by a grant from the NATIONAL RESEARCH COUNCIL.
[3] Shull, A. F., *Zeit. ind. Abst. Vererb., Berlin*, **57**, 92–111 (1930).
[4] Shull, A. F., *Amer. Nat., New York*, **65**, 469–473 (1931).
[5] Shull, A. F., *Ibid.*, **66**, 385–419 (1932).
[6] Shull, A. F., *Roux's Arch. f. Entwick. d. Org.*, **115**, 825–851 (1929).

THE CELLULAR TRANSMISSION OF NEUROHUMORAL SUBSTANCES IN MELANOPHORE REACTIONS

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Read before the Academy, November 15, 1932

The object of this paper is to point out a probable means of neurohumoral transmission other than that afforded by the blood and the lymph (Parker, 1932). The conditions are observable in the reactions of the melanophores in fishes. These animals, as is well known, may change the tint of the skin by expanding or contracting their dermal melanophores. If a short transverse cut is made near the root of the caudal fin of the common chub, Fundulus heteroclitus, a denervated area will be produced that will reach from the cut to the hind margin of the tail. After the cut is made the melanophores of this area quickly expand and the area is noticeable as a dark stripe running the length of the tail. This stripe gradually fades out in a few days—more rapidly when the stripe is narrow than when it is broad. If a fish of light tint whose stripe has disappeared is placed on an illuminated dark background, the body of the fish becomes rapidly dark. In such a fish the stripe will at first stand out as a light one and then in the course of time it will darken till it is no longer distinguishable from the rest of the tail. If such a dark fish is then put on a light background, the body of the fish quickly becomes light and the stripe then appears as a dark one in a light tail. This dark stripe will then gradually lighten till it attains the tint of the rest of the tail. Such changes in Fundulus can be produced again and again.

These observations confirm and extend in certain particulars the earlier

ones of Mills (1932b) who has also shown (1932a) in a very conclusive way that the melanophores in the tail of Fundulus have a double innervation, one set of nerve fibers controlling contraction and another set expansion. She has likewise shown (1932b) that in this fish the influence of the nerve fibers on the melanophores is in all probability exerted through substances secreted by the nerve terminals, an expanding neurohumoral substance from the expanding fibers and a contracting one from the contracting fibers. From this standpoint the obliteration of the stripes in the tests already described would result from the penetration of an opposing substance from the surrounding area into the denervated region, and one of the objects of the present paper is to record the remarkable slowness of this process.

Although the general body tint of a number of Fundulus was found to change from light to full dark in from 1.6 to 1.9 hours, the light stripes on their tails from a cut 1 millimeter wide required from 17 to 27 hours to make the corresponding change. Assuming this change to result from the penetration of a dark-inducing substance into the stripe from each of its sides, it is obvious that this substance must travel at a very slow rate, only half a millimeter in from 17 to 27 hours. A similar condition is to be found in the change from dark to light when the general body adjusts itself in from 4 to 5 hours but the stripe requires from 18 to 31 hours for the corresponding change. Here, too, we are forced to admit a very slow rate of transmission.

That such changes are not necessarily so slow can be shown by tests with adrenalin. If a small amount of adrenalin is injected into a fish whose body and stripe are both dark, the whole animal, body and stripe alike, become light in from ten to fifteen minutes. And if a similar injection is made into a light fish with a dark stripe on its tail, the stripe disappears in about the same time, the rest of the body remaining continuously light. In such tests the adrenalin is carried from the region of injection to the melanophores by the blood and the lymph and quickly reaches these color cells irrespective of whether they are in a part of the general surface of the fish or in the denervated stripe on its tail. The shortness of the time (10 to 15 minutes) required for the adrenalin to act on the melanophores of the stripe is in strong contrast with the great length of time (18 to 31 hours) needed for the action of the contracting neurohumor. The disparity between these two periods, 10 to 15 minutes and 18 to 31 hours, is so great, as to suggest an entirely different means of transmission in the two instances, a suggestion that also holds for the expanding neurohumor. It does not seem conceivable that the two neurohumors can be transmitted by blood and lymph whose flow even at their slowest would not be so retarded as is indicated by the records given. Much more likely is it that the neurohumors are handed on from the

adjacent innervated region into the denervated one through some other medium than blood and lymph and such a medium may well be the tissues themselves whose cells next the nerve terminals of the innervated area may take up the neurohumor there produced and pass it on either through their cell sap or their outer lipoid coverings to other cells more nearly within the denervated stripe. Thus the neurohumor would make its way from the nerve terminals of the adjoining region to the denervated melanophores by steps that would of necessity be time-consuming and consequently consistent with the intervals observed as contrasted with what has been noted for transmission by blood and lymph. I, therefore, conclude that in Fundulus the neurohumors for the melanophores spread by tissue, probably cellular, means and hence with great slowness.

The explanation of neurohumoral spread just put forward is quite in accord with what must occur rather extensively in many of the lower animals as, for instance, in the coelenterates. In such animals as sea-anemones, coral polyps, hydroids and the like, the wall of the body, which may be relatively thick, is composed of two cellular layers, an inner entoderm and an outer ectoderm separated by a firm supporting lamella. Only the entoderm is next the digestive cavity and hence only its cells are in a position to absorb nourishment directly from the supply of digested food elaborated in that cavity. The ectoderm, on the other hand, a layer of great activity from the standpoint of both muscles and glands, can gain its nourishment only by having the digested materials passed on to it through the entoderm and the intervening supporting lamella. Such a transmission seems to be a necessary part in the economy of such creatures and must be accomplished by the tissues of these lowly animals in much the same way as has been suggested for the transmission of neurohumors in the tail of Fundulus. The coelenterates possess neither blood nor lymph and the nourishment of their parts not next the digestive cavity must of necessity depend upon tissue or cellular transmission. From an evolutionary standpoint this type of transmission unquestionably antedates that of blood and lymph and must be looked upon as the original method of transmitting materials, a method still of first importance among primitive types and retained to a significant extent even in the vertebrates.

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PRELIMINARY ACCOUNT OF DEEP SEA DIVES IN THE BATHYSPHERE WITH ESPECIAL REFERENCE TO ONE OF 2200 FEET

By William Beebe

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Read before the Academy, Tuesday, November 15, 1932

1. *Introduction.*—In the course of the work of the Department of Tropical Research of the New York Zoölogical Society during the last four years off the southern coast of Bermuda, we have made the following investigations in or very close to an eight mile circle, the center of which is at 32°12′ North Latitude and 64°36′ West Longitude, nine and one quarter miles south-southeast of Nonsuch Island, Bermuda:

Net Hauls:

1929, 1930, 1931. 1350 nets. Surface to 1200 fathoms.

Bathysphere Dives:

Mr. Otis Barton accompanied me on all of these dives.

1930:

Contour Shore Dives over Insular Shelf:

80 feet	0.75 miles south of Gurnet.
120 feet	0.75 miles south of Gurnet.
210 feet	2 to 3.25 miles south of Nonsuch.
350 feet	1.75 miles south of Gurnet.

Open Ocean:

250 feet	5.5 miles south of Nonsuch.
800 feet	10 miles south of Nonsuch.
800 feet	5 miles south of Nonsuch.
800 feet	6.5 miles south of Nonsuch.
1426 feet	5.75 miles south of Nonsuch.

1932:

Contour Shore Dives over Insular Shelf:

50 feet	1.65 to 2.1 miles south of Nonsuch.
80 feet	0.2 to 1.1 miles south of Nonsuch.
250 feet	2.45 to 2.9 miles south of Nonsuch.
290 feet	0.5 to 2.4 miles south of Nonsuch.

Open Ocean:

1000 feet	3.5 to 6.0 miles south of Nonsuch.
2200 feet	5.0 to 5.5 miles south of Nonsuch.

2. *Physical Conditions at the Greatest Depths.* (*a*) *Sunlight.*—In my report on the 1930 dives[1] I gave the spectroscope report from the surface to 800 feet. At this depth the spectrum showed as a narrow band centering at the wave length 520 mμ. In Hulburt's technical analysis of these observations[2] he says, "Using the light absorption coefficients of sea water as measured in the laboratory and the Ramon-Einstein-Smoluchow-

ski theory of the scattering of light in liquids, it is found that the spectrum of the daylight at 800 feet in the sea has a maximum brightness at about 500 mμ; this agrees well enough with the observation."

In the course of the half mile dive, although my eyes were perfectly dark adapted, I could detect not the faintest glimmer of light from 1700 feet down. So as far as the human eye was concerned, conditions of absolute darkness existed at these deeper levels.

(*b*) *Temperature.*—Records were as follows:

800 feet	Inside Bathysphere	75° Fah.
2200 feet	Inside Bathysphere	70° Fah.
800 feet	Outside Bathysphere	65° Fah.
2200 feet	Outside Bathysphere	53° Fah.

This record of 53° Fah. was read through the quartz window on an ordinary thermometer.

The *Atlantis* made a temperature record in this area in August of 50.5° at a depth of 2622 feet, and we have two September readings in different years of

53.7° at 2400 feet
55° at 2700 feet

(*c*) *Pressure.*—Inside the Bathysphere we had, of course, no means of recording the increasing pressure. At the end of the several two-hour dives, when the wing bolt was removed on deck, after two or three minutes of gradually escaping air under pressure, the final blowout was less severe on our ears than from a descent to six fathoms in the diving helmet.

Our careful records with a deep-sea pressure gauge in this area give the usual mathematical ratio of increase, as known for the deep sea in general. The pressures withstood by the Bathysphere were as follows:

	POUNDS PRESSURE PER SQUARE INCH	TONS PRESSURE ON EACH WINDOW	TONS PRESSURE ON SPHERE
800 feet	370.7	5.26	1910
2200 feet	993.7	14.06	5120

(*d*) *Clarity of Observation.*—The fused quartz windows and the clarity of the deeper layers of the ocean combined to give unexpected clearness. Our 1000-watt electric light made a bright swathe through the blackness, conservatively estimated at 30 feet.

The upper 200 to 300 feet were the most turbid, the increase in transparency being especially noticeable from 500 feet down to where the blue blackness made all observation depend upon our occasional use of the electric light, and the illumination of the organisms themselves.

3. *Biological Observations.*—For purposes of comparison with my observations from the Bathysphere I append a list of fish taken in this area in 1350 nets. It is slightly incomplete, as a few groups, such as the Apodes and many pelagic forms, have not yet been studied.

TRAWLING RECORDS OF FISH FROM 0 TO 400 FATHOMS

FATHOMS	0	25	50	100	200	300	400	TOTAL 0–400 FATH.	TOTAL ALL DEPTHS	% 0–400 FATH.
FEET	0	150	300	600	1200	1800	2400			
Bathytroctes drakei							1	1	27	4
Stomias brevibarbatus							1	1	22	5
Stomias ferox						5	14	19	97	20
Bathophilus brevis						1		1	3	33
Bathophilus longipinnis							1	1	2	50
Bathophilus metallicus						1	3	4	20	20
Chirostomias pliopterus						1		1	6	17
Eustomias larvae	1							1	5	20
Lamprotoxus angulifer							1	1	4	25
Leptostomias ramosus						1		1	12	8
Melanostomias spilorhynchus	1						5	6	55	11
Photonectes dinema						1	1	2	26	8
Photonectes intermedius							1	1	5	20
Photonectes leucospilus						3		3	12	25
Photonectes parvimanus						1		1	6	17
Astronesthes gemmifer							2	2	8	25
Astronesthes niger						1	2	3	51	6
Stylophthalmus		1	2	13		1	2	19	46	41
Chauliodus danae						12	49	61	374	16
Chauliodus sloanei			2			50	43	95	412	23
Cyclothone microdon						416	1395	1811	57228	3
Cyclothone signata					31	6294	4014	10339	36861	28
Cyclothone pallida						2	20	22	505	4
Gonostoma elongatum							2	2	38	5
Yarrella blackfordi							1	1	5	20
Ichthyococcus ovatus						19	18	37	198	19
Vinciguerria attenuata						33	49	82	218	38
Argyropelecus aculeatus	1					22	27	50	135	37
Argyropelecus affinis							2	2	2	100
Argyropelecus hemigymnus						70	33	103	294	35
Argyropelecus sladeni					1	10	5	16	42	38
Argyropelecus larvae				2	4	184	121	311	638	49
Sternoptyx diaphana	1		2	12		25	83	123	1323	9
Leptocephalus	7	3	5	16	5	5	4	45	210	21
Serrivomer			1		1	15	15	32	149	21
Lestidium intermedium				3		2	2	7	19	37
Lestidium speciosum						1	4	5	57	9
Sudis bronsoni						5	17	22	668	3
Evermannella balbo							1	1	8	12
Evermannella melanoderma						1	1	2	37	5
Diaphus dofleini						13	40	53	192	28
Diaphus fulgens						8	8	16	93	17
Diaphus gemellari						2	2	4	27	15
Diaphus hypolucens							1	1	5	20
Diaphus macrophus						3	23	26	293	9
Diaphus metopoclampus						1	2	3	13	23
Diaphus rafinesquei							3	3	134	2
Lampadena braueri						1		1	54	2

TRAWLING RECORDS OF FISH FROM 0 TO 400 FATHOMS (*Continued*)

FATHOMS	0	25	50	100	200	300	400	TOTAL 0–400 FATH.	TOTAL ALL DEPTHS	% 0–400 FATH.
FEET	0	150	300	600	1200	1800	2400			
Lampanyctus crocodilus						2		2	95	2
Lampanyctus cuprarius			1			1	7	9	204	4
Lampanyctus elongatus							1	1	11	9
Lampanyctus photothorax						6	35	41	891	5
Lampanyctus pusillus						23	94	117	942	12
Lampanyctus subpectoralis					1	13	40	54	153	35
Lampanyctus supralateralis							5	5	27	19
Lampanyctus townsendi							7	7	879	0.8
Myctophum affine							1	1	37	3
Myctophum benoiti						5	16	21	1294	2
Myctophum coccoi						3	17	20	1 5	12
Myctophum fibulatum							1	1	8	12
Myctophum hygomi						1	17	18	130	14
Myctophum imitator							8	8	29	28
Myctophum laternatum				2	1	49	191	243	2833	9
Myctophum macrochir						3	9	12	167	7
Myctophum reinhardti				1		3	3	7	71	10
Myctophum valdiviae						87	178	265	839	32
Omosudis lowi						1	6	7	293	2
Bregmaceros macclellandii			1					1	34	3
Physiculus kaupi				1				1	1	100
Etropus	16	2	1			1	1	21	33	64
Cyttus hololepis						1		1	1	100
Anoplogaster cornutus		1	4					5	22	23
Melamphaes microps						3	27	30	967	3
Melamphaes mizolepis						1	4	5	65	8
Melamphaes robustus				1				1	306	0.3
Melamphaes larvae			3			11	55	69	600	12
Diretmus argenteus						1		1	3	33
Gempylidae	21	11	9	1	6	7	1	56	216	26
Brama raii	1	21	2	1		1	1	27	28	96
Pteraclis		1				1		2	29	7
Cubiceps	1	5	2	17	3	14	3	45	52	87
Psenes	1						1	2	22	9
Zonichthys falcatus							1	1	1	100
Oxyodon							2	2	51	4
Remora	1						1	2	2	100
Pseudoscopelus stellatus		2	1			2		5	8	63
Fierasfer larvae			1					1	3	33
Lyosphaera	3	2	14		2	4	2	27	66	41
Mola mola	2	21						23	30	77
Cryptosparas cousii	2							2	24	8
Melanocetus murrayi	1	1						2	12	17
Larval pediculates	20	4	2	1			4	31	100	31

(*a*) *Activity of Fish.*—It has been thought that the activity of fish and other organisms is less at great depths than at the surface, and the bizarre shapes, globular and angular, would seem to support this theory.

In all cases where I was able to see organisms in motion there was no hint of slowness, other than that imposed by the absence of stream lines. This was fore-shadowed by the fish up to twelve inches in length, from half a mile to a mile, which we have kept alive in refrigerators and photographed. They have swum and twisted and snapped with as much accuracy of balance and speed as surface fish.

(*b*) *Illumination.*—Heretofore we have had three sources of information with regard to the illumination of deep-sea organisms:

1. Examination of the photophores of preserved or recently dead specimens.
2. Dark room observations on the light of fish brought up alive.
3. Comparison with luminous terrestrial Coleoptera and other forms.

I have elsewhere[3] described what I believe to be several distinct uses of illumination in living *Myctophum coccoi*, and during three years of trawling off Nonsuch we have made many records of flashes or more continuous lighting, in abyssal fish which have survived from ten minutes to as many hours.

Under cloudy conditions I have detected flashes of light in my Bathysphere dives as far up as 400 feet. From 1700 feet down, animal light is the only external source of illumination.

The non-halation of these lights was marked throughout. This must be due to the clarity of the mediums traversed by the light. Several times there were flashes from unknown organisms so bright that my vision was confused for several seconds. Often the abundance of lights was so great that the comparison is unavoidable with the stars on a clear, moonless night. The constant movement tended to confuse direct, concentrated vision, but by continual effort I managed to follow definite constellations, and in almost every case could make out the outline of the fish.

Occasionally the head of a fish would appear conspicuously against the surrounding black, illumined by some unknown source of indirect lighting. Eyes especially stood out with no definite source of light visible. When teeth were thus silhouetted I knew it was from a luminous mucous which covered them. Cheek lights flashed and dimmed, or vanished altogether, showing some control other than the usual disappearance into an opaque epidermal trench.

The visibility of the thousands of minute photophores scattered over the surface of the body of Melanostomids was unexpected. These are inconspicuous, minute, and in living, trawled specimens show no sign of light.

In the last minute or two of observation I was able to connect a bobbing bluish light as the terminal illumination of a long barbel belonging to the faint outline of a fish passing over it.

The color of the lights, in order of abundance, was greenish, bluish and rosy, in all cases the tint being a pale one.

Once a wavering spot of greenish light, almost a half-inch across, came straight toward the window and where it struck the quartz burst into innumerable, slow-dying flares, revealing no connecting tissues, giving no slightest hint of phylum. On the other hand a jellyfish would pass with every detail thrown into contrast by the many green lights given off by tissues or ingested food.

In a few cases I saw an entire fish evenly illumined with no foci of photophores. This was doubtless from some epidermal, phosphorescent slime or mucous

(*c*) *Abundance and Size of Fish Observed.*—Comparison of the average number of deep sea fish taken in each of 1350 nets drawn in this area with detailed observations in the Bathysphere reveal a very marked discrepancy. This can be explained only by the imperfection of our modern trawling apparatus. One- and two-meter silk nets can be drawn at a rate of only two knots per hour, and this apparently allows all the larger and more active forms to escape.

It is evident that our vertical distribution tables, based, as they must be, on trawling results, represent only an approximation of the truth.

I saw illuminated fish up to six feet in length, larger than oceanographers have ever been able to capture.

Our trawling records show the following data relating to the relative abundance of fish taken at 0–400 fathoms:

Total number of nets drawn 0–1200 fathoms	1350
Total number of nets drawn 0–400 fathoms	297
Ratio	22%
Total number of species of deep sea fish taken	264
Number of species taken 0–400 fathoms	92
Ratio	34%
Total specimens of 92 species, taken 0–1200 fathoms	112,213
Total specimens of 92 species, taken 0–400 fathoms	14,546
Ratio	13%

(*d*) *Identification.*—This is the most important and the most delicate phase of the present work. For authenticity and accuracy it requires not only familiarity with the abyssal fish of this vicinity and their photophores, but the resolving of living constellations presented to the vision for five to ten seconds, or less.

It required several dives in 1930 before I could distinguish Cyclothones from worms of equal size, while constantly recurring, conspicuous groupngs of lights defied classification even as to phylum.

The great number of Pteropods, chiefly *Cavolinia* and *Limacina*, ob-

served is not remarkable when we remember that this area of sea bottom affords the only example of pteropod ooze in the North Atlantic.

Pyrosoma, Jellyfish, strings of Siphonophores and Squids were the most abundant invertebrates, with occasional large masses of Shrimps, all often brightly illuminated.

At 1500 feet I saw six large, red Prawns, *Notostomus* or *Gnathophausia*, faintly illumined with lights emanating from their own body, also seen in the electric beam. The trawling records show the maximum occurrence of these crustacea at 4800 feet, while two only have been taken as high up as 3600 feet.

From the list of fish trawled above 400 fathoms we note the absence of certain important families or genera: *Alepocephalidae*, *Bathylagidae*, *Brotulidae*, *Gastrostomus*, *Cetomimus*, *Caulolepis*, *Chiasmodon* and all large "black fish" such as *Melanostomiatidae*, *Chauliodus* and adult *Pediculata*. I observed a number of these at very shallow depths.

The object of this brief, preliminary review seems best served by a categorical list of some of the most important fish observed, arranged by depth:

SURFACE TO 20 FEET:

Twice I have seen flying-fish pass, and vanish into the air above the quilted ceiling of water above me.

50 FEET:

Psenes, several times, coming close to my bait.
Bonitos.

80 FEET:

Small *Leptocephalus*.

100 FEET:

Puppy-shark (probably *Carcharias platyodon*) and Pilot-fish (*Naucrates ductor*).
Sardinellaaurita
Trigger-fish.
Leptocephalus, twelve-inch.

200 FEET:

Seriola, six-inch.
Psenes.
A Porpoise, the only mammal seen; swam past, going obliquely downward, with possibly another in the distance.

300 FEET:

Psenes, close to window.
Pilot-fish at bait.

400 FEET:

Myctophidae.—species?
Small Puffers.
Cyclothone.—Whereas Cyclothones compose four-fifths of all the fish trawled above 400 fathoms, yet I am convinced they do not live in schools; there is too great a

uniformity of numbers in each net drawn. From the Bathysphere these fish were with difficulty distinguishable from invertebrates of similar size. Only when they came close could I be certain, and I never saw more than five close together. By reference to the list of fish, in this and other cases, it will be seen how many species I observed far above their usual capture levels.

Psenes.

Eels, probably *Nemichthys*, six-inch, silvery.

Myctophidae, school of about thirty.

On a cloudy day, saw first flash of luminescence at this level.

500 FEET:

Transparent fish, with food conspicuous, three-inch.

A two-foot *Coryphaena* swam straight toward the window.

600 FEET:

At this depth I saw, for the first of several times, large bodies moving in the distance. These seemed uniformly pale or white, and may have been either squid or fish of great size. Mr. Barton and I both saw them.

Leptocephalus at bait.

Seriola-like fish, five-inch, very deep, with black fins. No known species.

Six Puffers, four-inch, quite unlike any member of their family known to me.

650 FEET:

Two eight-foot, dusky sharks swimming slowly around Bathysphere. This is the lowest depth at which sharks were seen.

Argyropelecus in a small school. Lights faint and completely obliterated in the electric beam.

700 FEET:

Twelve four-inch fish swimming upright.

Very large forms moving in distance.

Argyropelecus.

Cubiceps close to glass.

Two Rudder-fish (*Seriola zonata*), like those seen at 300 feet in 1930.

750 FEET:

A three-foot Melanostomid-like fish. It had the usual two rows of lateral lights, but a long, slender, Macrourid-like tail.

Three transparent fish, three-inches, close to window.

Seven *Myctophum coccoi.*

Two two-foot *Serrivomer* eels.

Melamphid, close to glass, three-inch. For several seconds it hung motionless before me in the beam.

800 FEET:

Several four-inch, dark, very deep fish around bait.

Two *Cyclothone* very close to glass.

Twenty *Argyropelecus* swimming obliquely down, close together.

Idiacanthus, six-inch, clearly seen, elongate, black, pale cheek light. (Uppermost trawling record 3000 feet.)

Three *Diaphus*, head-lights plainly seen; three-inch.

Eels, unknown species, two close together, one dark, one light.

Two more specimens of *Myctophidae*, one six-inch.

Eustomias-like fish, five-inch.

Thirty *Cyclothone* in loose group, drifting past as we descended, two or three in view at a time.

Two *Leptocephalus*, close together, twelve- to fourteen-inch.

Eleven *Myctophum coccoi*, lateral lights dim but steady; ventral flash seen twice, pale blue.

Some large, pale white body in distance.

875 FEET:

As we descended, saw brightest flash ever seen. It seemed to go on and off twice; central spark distinct the first time; very bright, blinding; whole foreground illumined. The creature had vanished when the electric beam was thrown on.

1000 FEET:

Six *Argyropelecus*.

Two Eels, two-foot, swam past. One returned and kept in view for twenty feet.

Some large body, perhaps Squid, in distance.

Serrivomer, two-foot, moving slowly.

1050 FEET:

About twenty small *Argyropelecus*.

1100 FEET:

Twelve-inch *Melanostomidae*. Body covered with minute lights.

Three *Macrouridae*, six inches long, with long, rat tails, large heads and at least six good-sized lights. Swam twice around bend of hose and through beam.

1200 FEET:

Idiacanthus again.

Two *Astronesthes*, close against glass and in beam.

Melamphaes in beam, three-inch. Seemed to glow dully after they had swum out of beam.

1225 FEET:

Several hundred double lights, one above the other. No organism visible.

1250 FEET:

Stomias, five-inch.

Argyropelecus.

1300 FEET:

Melanostomid-like fish, two lateral rows of lights, and body covered with pin-pricks of light; two-foot.

1400 FEET:

At least forty small, pale, four-inch fish, glowing clearly, no distinct lights. Closely resembled *Scopelarchus*. A *Leptocephalus* passed, clearly lighted by their light.

1500 FEET:

Four fish, eight-inch, with orange lights on head, and bluish white on body. The light persisted even in the electric beam. Jaws short and very wide; two fangs depending from upper jaw; none from lower. Not like any form known to me.

Serrivomer, two large, two small.

1700 FEET:

Biggest Eels yet in beam. Four or five, about three feet long. Neither *Serrivomer* nor *Nemichthys*.

Chauliodus. An example of perfect identification. Seven, all headed one way.

Eyes shone with dull glow, from indirect photophore light; bodies covered with multitude of small lights. One dashed toward me, and head-on I could distinguish the flash of long fangs, although I do not know whence the illumination came. It turned, close to window, and for a second was silhouetted clearly, showing hexagonal scales, and then vanished. Remaining six had meanwhile disappeared, leaving in view only an elongate series of dull golden siphonophores.

1800 FEET:

Melanostomids with double, lateral rows of lights distinct.

Melamphid-like fish, twelve-inch. In beam for two seconds. Head large and very rugged.

1825 FEET:

Sternoptyx, five, large and brilliant, close together. Photophores blue, not purple. One dashed into beam close to window. Very active.

1850 FEET:

Single large fish, about four feet long, very deep, almost round in outline. No lights; seen in beam.

1900 FEET:

Adult Pediculate, in general *Melanocetus* rather than *Cryptosparas* type; two-foot; long, unlighted tentacle, visible in beam, but several foci of dim lights elsewhere on body. Opened mouth and partly closed it twice before it disappeared.

2000 FEET:

Five *Sternoptyx*.

Large, Barracuda-like fish, its lights more green than any seen before.

2100 FEET:

Two large, elongate, Barracuda-like fish, larger than any others seen. They passed within eight feet, and were fully six feet long. No lights visible on head, yet eye was clearly distinct, and outline faintly; a single row of strong, pale blue lights along body. Mouth and fangs illumined either by mucous or by indirect internal lights on branchiostegals. General shape of Barracuda, with deeper jaws open all the time. There were two barbels, each with two, separate, luminous bodies, the anterior more red than the posterior. These twitched and jerked along beneath the fish. One undoubtedly arose from a mental base, the other so far back that its origin must have been from the anal fin.

2200 FEET:

Four fish, twelve inches long, silvery in beam.

A six-inch fish passed slowly. Could see upper and lower sides as it turned partly over. It was very deep, with outlines visible from some indirect lighting. When head-on all illumination vanished.

4. *Contour Shore Dives.*—These are still being made, so any account must be only preliminary. Their object is to trace the littoral or shallow water Bermuda fauna to the mid-depths. Eight of these dives have been made, from 50 to 350 feet. Near the latter depth the bottom fell away so sharply that it could not again be recovered, the risk of the Bathysphere striking against reefs being too great.

In general, the bottom, for a mile off shore, resembles the present shore

reefs, the fish of known species becoming larger as we go outward. Some of the most abundant mid-water types, such as *Chromis cyaneus* and *Sardinella aurita* are rare or unknown in-shore.

Beyond this and down to 200 feet, the bottom is less rugged, and the seafans and plumes smaller. Then comes an abrupt range; in one spot, over which the Bathysphere had to be drawn, 50 feet in height. Beyond this comes a long, sloping beach, of water-worn pebbles and stones, wholly without living growths or fish, and ending in wide stretches of white, rippled sand. It is probable that this is the beach of the last low ocean level of the glacial period.

The slow seaward drift of the tug, and the average level of the Bathysphere of 10 feet above the bottom, enable us to see all fish, down to two inches, with perfect clearness.

In mid-summer, with a day of brilliant sunshine and with clear water, it will be quite possible to follow the volcanic slopes down for many hundred feet farther without losing sight of the bottom.

[1] *N. Y. Zoöl. Soc. Bull.*, **33**, No. 6, 227.

[2] *Jour. Opt. Soc. Amer.*, **22**, No. 7, 408–417.

[3] The Arcturus Adventure, pp. 214–218.

A STEP-POLYGON OF A DENUMERABLE INFINITY OF SIDES WHICH BOUNDS NO FINITE AREA

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The problem of Plateau was completely solved by J. Douglas,[1] who proved the existence of a minimal surface bounded by any given Jordan curve.

The solution divided itself into two parts, the first referring to a contour which spans at least one surface of finite area, after which by a limit process the existence proof was extended to an arbitrary Jordan curve Γ which spans no finite area: every surface bounded by Γ has infinite area.

The question was thus raised as to the effective existence of the second type of contour. An example (P), based on Peano curves in the xy-plane, was constructed by the joint authors of this note,[2] and the basis of proof briefly indicated as consisting in infinite area of the horizontal projection of (P). A few further remarks concerning this example will be found at the end of this note.

Our main purpose in this communication is to give a simpler example in the form of a step-polygon of a denumerable infinity of sides, together

with all the details of proof. This step-polygon may be considered as more simple than, for instance, many rectifiable curves—showing that one must be careful not to overestimate the generality of any treatment of the Plateau problem that restricts itself to the case of a finite-area-spanning contour.

1. *Description.*—To arrive at the example, we begin by constructing a "skyscraper" of an infinite number of floors, and with infinite floor space, but finite height. The ground plan (horizontal projection) of the skyscraper is shown in figure 1. The sides of the squares, which crowd into the left rear corner, are

$$\frac{1}{\sqrt{n}} \quad (n = 1, 2, 3, \ldots \text{ ad infin}),$$

and each square represents a floor. The total floor space is the sum of the divergent harmonic series:

$$\sum_{n=1}^{\infty} \frac{1}{n} = +\infty.$$

The skyscraper is formed by raising the nth square a vertical distance

$$\frac{1}{2^{n-1}},$$

so that the total height is unity.

We next take the nth floor and divide it into

$$2^n + 1$$

equal rectangular strips. Then we construct a broken line as indicated in figure 2, running back and forth along the sides of these rectangles. Since $2^n + 1$ is odd, it is evident from the mode of construction that the broken line will end at the left forward corner B_n of the square if it starts at the left rear corner A_n.

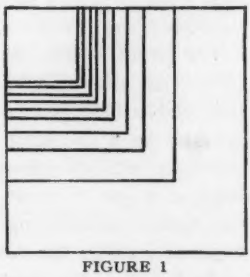

FIGURE 1

We thus have a rectangular broken line in each floor. These we connect by joining A_{2m} to A_{2m-1} with a vertical line segment, and B_{2m} to B_{2m+1} with a vertical segment $B_{2m}C_{2m+1}$ to the level of the $(2m + 1)$th floor followed by the horizontal segment $C_{2m+1}B_{2m+1}$.

We now have a Jordan arc in the form of a rectangular broken line consisting of a denumerable infinity of segments, going from B_1 (0,1,0) to A_∞ (0,0,1). This may be completed to an infinitely many sided closed Jordan step-polygon by the line segments B_1C, CA_∞, where C is the point (0,1,1).

Our example is now finished.

2. *Proof.—Cylindrical Pipes.*—About each of the transverse, or long, segments of the broken line which traverses the nth square—except the last segment, ending at B_n—let a cylinder of revolution be constructed as follows. The axis of the cylinder shall be one-half the length of the segment, symmetrically placed with respect to the ends (from the one-quarter division point to the three-quarters point); the radius R_n shall be one-half the width of a rectangular strip, that is:

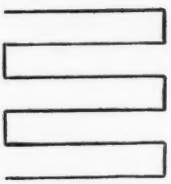

FIGURE 2

$$R_n = \frac{1}{2(2^n + 1)\sqrt{n}}.$$

Since the distance between the nth and $(n + 1)$th floors is $\frac{1}{2^n}$, each cylinder reaches less than half-way to the floor next above, and *a fortiori* less than half-way to the floor next below; therefore the cylinders *do not overlap*, though (what is of no importance) those on the same floor are externally tangent.

We shall need the fact that the total area of the generating rectangles of the cylinders on the nth floor is one-fourth the area of that floor, $= \frac{1}{4n}$.

Next we need the following lemma.

LEMMA. *Consider a right circular cylinder with axis AB. If any simply connected surface is spanned by AB together with a curve joining A and B lying entirely outside the cylinder, the area of the portion of the surface interior to the cylinder is at least equal to that of the generating rectangle of the cylinder.*

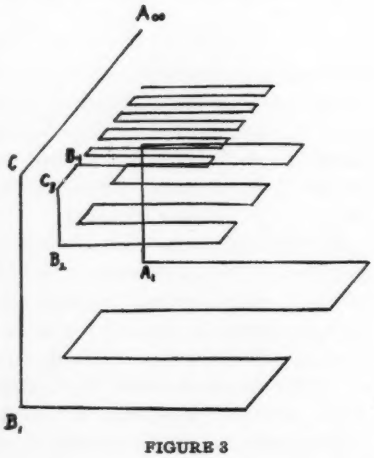

FIGURE 3

The proof results immediately by circular projection of the portion of surface interior to the cylinder on a meridian plane, an operation which obviously diminishes area (or, at most, leaves it the same), multiplying each element of area by the cosine of the angle between the tangent plane to the element and the meridian plane through the point where the element is located. By the same proof, the theorem extends to any solid of revolution, the minimum intercepted area being half a meridian section.

Infinite Area.—Consider now the cylindrical pipes on the nth floor.

The sum of the areas of their generating rectangles is, as has been remarked, $\frac{1}{4n}$; consequently the portion of any simply connected surface Σ bounded by the step-polygon intercepted by these cylinders is at least $\frac{1}{4n}$ in area. Since the cylinders on different floors do not overlap, the area of the portion of Σ intercepted by all the cylinders is at least $\frac{1}{4}$ the sum of the divergent harmonic series; hence

$$Area\ of\ \Sigma = +\infty,$$

which was to be proved.

The infinite part of the area of the minimal surface M determined by the step-polygon is all bunched up in the vicinity of the singular point A_∞, summit of the "skyscraper." If, in traversing the boundary of M, we make a detour around A_∞, passing between two boundary points on opposite sides of A_∞ by any arc lying, except for its end-points, in the interior of M, then the area of the intercepted part of M will be finite.

3. *Remarks on the Example* (P).—If the reader is interested in the details of proof for the originally given contour (P), he should find little difficulty in supplying them on the model of the foregoing discussion. In fact, if the Peano curve (P') which is the xy-projection of (P) is replaced by a sufficiently advanced polygonal approximation,[3] the following hint should suffice to prove that even the simplified version of (P) so resulting (skew polygon of a denumerable infinity of sides) can span no finite area.

Hint.—A square column, tall, with very small base, is traversed by a line segment σ from a point well up on a lateral edge to a point at about the same level on the diagonally opposite edge. Then the area intercepted by the column on any surface bounded by a contour consisting of σ together with an arc lying entirely outside the column is at least equal to the area of one of the 45° right triangles into which the base is divided by a diagonal.

[1] "Solution of the Problem of Plateau," *Trans. Amer. Math. Soc.*, **33**, 263–321 (1931).

[2] Loc. cit., p. 320.

[3] F. Klein, *Elementarmathematik vom höheren Standpunkte aus*, 3d ed., Berlin, 1928, p. 119.

CRESCENT-SHAPED MINIMAL SURFACES

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1. *The Problem of Plateau for Crescent-Shaped Minimal Surfaces.*—The problem of Plateau is to prove the existence of a minimal surface with a given boundary. A minimal surface is one definable by the Weierstrass formulas

$$x_i = \Re F_i(w), \quad \sum_{i=1}^{n} F_i'^2(w) = 0 \quad (i = 1, 2, \ldots, n). \tag{1.1}$$

The author has given a solution of the Plateau problem for two contours,[1] by methods which are a natural generalization of those previously used by him to give the first complete solution of the Plateau problem for a single contour.[2]

It was assumed, in the treatment of the two-contour case, that the contours did not intersect one another. If, on the contrary, the contours have a single point in common, then we may obtain a minimal surface of the topological type of the region between two internally tangent circles; indeed, the minimal surface will be representable conformally on this region. Such a region we call a *crescent*, and the minimal surface representable conformally upon it *crescent-shaped*.

The purpose of the present note is to adapt the methods of the previous papers of the writer, cited above, to solve the Plateau problem for crescent-shaped minimal surfaces: *given two Jordan curves* Γ_1 *and* Γ_2, *with one and only one point* P *in common, to prove—under appropriate sufficient conditions—the existence of a crescent-shaped minimal surface bounded by* Γ_1 *and* Γ_2.

That some sort of restriction on the contours is necessary is evident from considering, for instance, two externally tangent circles in the same plane; obviously they determine no proper crescent-shaped minimal surface, giving rather the sum of the two circular discs. The sufficient condition established in this paper is that if $m(\Gamma_1, \Gamma_2)$ denote the minimum of crescent-shaped areas bounded by Γ_1 and Γ_2, and $m(\Gamma_1)$, $m(\Gamma_2)$ the minimum of simply connected areas bounded by Γ_1, Γ_2 separately, then

$$m(\Gamma_1, \Gamma_2) < m(\Gamma_1) + m(\Gamma_2) \tag{1.2}$$

(the relation $\leqq$ holds in any case). We also suppose that all three quantities m are *finite*, an assumption certainly verified if the contours are rectifiable.

2. *The Functional* $A(g_1, g_2)$.—If the crescent is subjected to an in-

version with the point of tangency of its bounding circles as pole, we obtain a strip bounded by two parallel straight lines; without loss of generality, we can assume this strip to be that bounded by the lines

$$(L_1) \quad z = \text{real, and } (L_2) \quad z = \text{real} + \pi i,$$

in the complex plane of z. The inversion, being a conformal transformation, will convert a conformal representation of the required minimal surface on the crescent into a conformal representation on the strip, and vice versa.

The next step is to adapt to crescent-shaped surfaces the functional employed in the author's treatment of the one- and two-contour cases of the problem of Plateau.

Let

$$x_i = g_{1i}(z), \quad x_i = g_{2i}(z) \quad (i = 1, 2, \ldots, n) \tag{2.1}$$

denote arbitrary parametric representations of Γ_1 and Γ_2, where z describes L_1 and L_2, respectively, the common point P of the two contours being always required to correspond to the point at infinity on each line. If

$$x_i = \Re F_i(w) \quad (w = u + iv)$$

denote the harmonic functions determined in the parallel strip S by the boundary values (2.1), these functions define a crescent-shaped harmonic surface bounded by Γ_1, Γ_2. Let the first fundamental form of this surface be

$$ds^2 = Edu^2 + 2Fdudv + Gdv^2,$$

then the fundamental functional is

$$A(g_1, g_2) = \int\int_S \tfrac{1}{2}(E + G)dudv. \tag{2.2}$$

This integral must be defined accurately as a limit; we construct the strip S_ϵ by removing a band of width ϵ from each edge of S, and define

$$A_\epsilon(g_1, g_2) = \int\int_{S_\epsilon} \tfrac{1}{2}(E + G)dudv, \tag{2.2'}$$

then

$$A(g_1, g_2) = \lim_{\epsilon \to 0} A_\epsilon(g_1, g_2).$$

It is not hard to prove that the integrand of A_ϵ stays uniformly bounded for all g_1, g_2 if ϵ is fixed > 0.

It is desirable to have a direct expression for A in terms of g_1 and g_2; this can be obtained by means of formulas established in Two Contours (§ 2). Let $G(x, y; u, v)$ denote the Green's function for the region S; then G can always be given the form

$$G(x, y;\ u, v) = \Re \log \frac{S(z, w)}{S_1(z, w_0)}, \tag{2.3}$$

where

$$z = x + iy, \quad w = u + iv, \quad w_0 = u - iv.$$

If

$$Z(z, w) = \frac{\partial}{\partial z} \log S(z, w), \tag{2.4}$$

and

$$P(z, w) = \frac{\partial}{\partial w} Z(z, w) = \frac{\partial^2}{\partial z \partial w} \log S(z, w), \tag{2.5}$$

then, with the help of Green's theorem, the explicit form for A is:

$$A(g_1, g_2) = \frac{1}{4\pi} \sum_{\alpha\beta} \int_{L_\alpha} \int_{L_\beta} \sum_{i=1}^{n} [g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2\ P(z, \zeta) dz\, d\zeta. \tag{2.6}$$

Here and elsewhere in this paper, integration on L_1 is to the right, on L_2 to the left.

It is to be observed that, although complex elements enter into this formula, the value of $A(g_1, g_2)$, according to (2.2), is always positive real.

The next step is to obtain explicitly the Green's function for the strip S. We state the result immediately:

$$G(x, y;\ u, v) = \Re \log \frac{\sinh \frac{1}{2}(z - w)}{\sinh \frac{1}{2}(z - w_0)}. \tag{2.7}$$

It will be an easy exercise for the reader to verify that this has all the requisite properties: regular harmonic in the strip S except at the one point w where there is a logarithmic singularity, reducing to zero on L_1 and L_2.

By comparison with (2.3),

$$S(z, w) = \sinh \tfrac{1}{2}(z - w), \tag{2.8}$$

and therefore, by (2.4) and (2.5),

$$Z(z, w) = \tfrac{1}{2} \coth \tfrac{1}{2}(z - w), \tag{2.9}$$

$$P(z, w) = \frac{1}{4 \sinh^2 \frac{1}{2}(z - w)}. \tag{2.10}$$

Hence, by substitution in (2.6),

$$A(g_1, g_2) = \frac{1}{4\pi} \sum_{\alpha\beta} \int_{L_\alpha} \int_{L_\beta} \sum_{i=1}^{n} [g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2 \frac{dz d\zeta}{4 \sinh^2 \frac{1}{2}(z - \zeta)} \tag{2.11}$$

The integral is improper, on account of the singularity of the integrand for $z = \zeta$, but always exists either as a finite positive quantity or $+\infty$; its value is to be found by integrating first with $|z - \zeta| \geqq \epsilon$, furnishing $\overline{A}_\epsilon(g_1, g_2)$, and then defining

$$A(g_1, g_2) = \lim_{\epsilon \to 0} \overline{A}_\epsilon(g_1, g_2).$$

By a formula of Two Contours [2.13, loc. cit.] and (2.9) above, the harmonic surface determined by g_1, g_2 is

$$x_i = \Re F_i(w)$$

with

$$F_i(w) = \frac{1}{2\pi i} \sum_\alpha \int_{L_\alpha} g_{\alpha i}(z) \coth \tfrac{1}{2}(z - w)dz + c_i, \qquad (2.12)$$

where c_i is a constant whose exact value is unnecessary.

We shall need too the formula, easily derived from the last one [cf. Two Contours, 2.16]:

$$\sum_{i=1}^{n} F_i'^2(w) = \frac{1}{2\pi^2} \sum_{\alpha\beta} \int_{L_\alpha} \int_{L_\beta} \sum_{i=1}^{n} [g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2 \frac{dzd\zeta}{16 \sinh^2 \tfrac{1}{2}(z - w) \sinh^2 \tfrac{1}{2}(\zeta - w)}. \qquad (2.13)$$

3. *Attainment of the Minimum of* $A(g_1, g_2)$.—Each of the sets $[g_1]$, $[g_2]$ of parametric representations of Γ_1, Γ_2, respectively, is compact. Therefore the composite elements $[g_1, g_2]$ form a compact set.

The integrand of A_ϵ in (2.2′) is uniformly bounded, and, under this circumstance, a theorem of Lebesgue permits us to pass to the limit under the integral sign. This is to say that A_ϵ is a continuous functional of g_1, g_2: if $\bar{g}_1 \longrightarrow g_1$, $\bar{g}_2 \longrightarrow g_2$, then $A_\epsilon(\bar{g}_1, \bar{g}_2) \longrightarrow A_\epsilon(g_1, g_2)$.

The integrand $\frac{1}{2}(E + G)$ being positive, the approach of A_ϵ to A when $\epsilon \longrightarrow 0$ is monotonic increasing; under this condition, the following lemma[3] enables us to affirm the lower semi-continuity of $A(g_1, g_2)$: *if a functional A on a Fréchet L-set can be expressed as the limit of a continuous functional* A_ϵ *which tends to A in increasing, then A is lower semi-continuous.*

From the compactness of the range $[g_1, g_2]$ and the lower semi-continuity of $A(g_1, g_2)$, it follows, as in the author's previous papers, that the minimum of $A(g_1, g_2)$ is attained for a certain (g_1^*, g_2^*); the proof is essentially the same as the Weierstrass proof of the attainment of the minimum of a (lower semi-) continuous function of a real variable on a closed interval, depending on the Bolzano-Weierstrass theorem expressing compactness: every infinite sequence of values of the argument (g_1, g_2)

contains a convergent sub-sequence, and on the definition of lower semi-continuity:

$$A(g_1, g_2) \leqq \liminf A(\bar{g}_1, \bar{g}_2) \text{ when } \bar{g}_1 \longrightarrow g_1, \bar{g}_2 \longrightarrow g_2.$$

4. *Exclusion of Improper Representations.*—We have next to show that the minimizing representation (g_1^*, g_2^*) is proper.

In the author's previous papers, the improper representations of a contour Γ have been classified as follows:

(a) A partial arc of Γ (Γ_1 or Γ_2) corresponds to a single point of L (L_1 or L_2).

(b) A partial segment of L corresponds to a single point of Γ.

(c) All of Γ corresponds to a single point of L and all of L to a single point of Γ.

Type (a) is excluded by the fact that then:

$$A(g_1, g_2) = + \infty,$$

for the integrand of (2.11) becomes infinite to the second order in the vicinity of the point of discontinuity, being asymptotically

$$\frac{l^2}{(z - \zeta)^2},$$

where l is the length of the chord of the arc of discontinuity of Γ. $l > 0$ because this arc is only a partial arc of Γ, and, by hypothesis, Γ has no double points.

Type (b) can be excluded by the mode of reasoning used in One Contour, § 18, based on a certain theorem of Fatou and Schwarzian symmetry—after it has been proved, as will be done in the next section, that

$$\sum_{i=1}^{n} F_i'^2(w) = 0.$$

It is in order to exclude type (c) that we need the condition (4.6) below, restricting the two contours.

Besides the functional $A(g_1, g_2)$, let us consider

$$A(g_1) = \frac{1}{4\pi} \int_{L_1} \int_{L_1} \sum_{i=1}^{n} [g_{1i}(z) - g_{1i}(\zeta)]^2 \frac{dz d\zeta}{(z - \zeta)^2},$$

$$A(g_2) = \frac{1}{4\pi} \int_{L_2} \int_{L_2} \sum_{i=1}^{n} [g_{2i}(z) - g_{2i}(\zeta)]^2 \frac{dz d\zeta}{(z - \zeta)^2};$$

these are the functionals appropriate to the construction of a simply connected minimal surface bounded by Γ_1 or Γ_2, respectively. Define the three positive numbers

$$m(\Gamma_1, \Gamma_2) = \min A(g_1, g_2), \tag{4.1}$$

$$m(\Gamma_1) = \min A(g_1), \quad m(\Gamma_2) = \min A(g_2),$$

the minima being relative to all possible parametric representations of Γ_1, Γ_2. Concretely, $m(\Gamma_1, \Gamma_2)$ is the lower bound of the areas of all crescent-shaped surfaces bounded by Γ_1, Γ_2, and $m(\Gamma_1)$, $m(\Gamma)$ the lower bounds of the areas of all simply connected surfaces bounded, respectively, by Γ_1, Γ_2; but we shall be concerned only with the definitions (4.1).

As stated in § 1, we assume that all three quantities (4.1) are finite.

If g_1 degenerates into a point p_1 on Γ_1, and g_2 is not degenerate, we can prove by reasoning similar to that of Two Contours, p. 342 (which we shall not repeat here), that

$$A(g_1, g_2) > m(\Gamma_1) + A(g_2),$$

whence

$$A(g_1, g_2) > m(\Gamma_1) + m(\Gamma_2). \tag{4.2}$$

If both g_1 and g_2 are degenerate, in points p_1 and p_2, respectively, not both coincident with the unique point P common to Γ_1 and Γ_2, then

$$A(g_1, g_2) = + \infty. \tag{4.3}$$

If p_1 and p_2 are both coincident with the point P, then

$$A(g_1, g_2) = m(\Gamma_1) + m(\Gamma_2). \tag{4.4}$$

This formula shows that always

$$m(\Gamma_1, \Gamma_2) \leqq m(\Gamma_1) + m(\Gamma_2). \tag{4.5}$$

Let us now introduce the assumption that we have the strict inequality:

$$m(\Gamma_1, \Gamma_2) < m(\Gamma_1) + m(\Gamma_2), \tag{4.6}$$

then it will be seen by the formulas (4.2, 3, 4) that the possibility of a minimizing representation of type (*c*) is excluded.

5. *Vanishing of the First Variation of* $A(g_1, g_2)$.—The functional $A(g_1, g_2)$ attaining its minimum for (g_1^*, g_2^*), its first variation must then vanish—a condition which will lead to

$$\sum_{i=1}^{n} F_i'^2(w) = 0, \tag{5.1}$$

proving that the harmonic surface determined by (g_1^*, g_2^*) according to the formulas (2.12) is minimal.

We employ the following variation of the independent variables:

$$z' = z + \tfrac{1}{2}\lambda \coth \tfrac{1}{2}(z - w), \tag{5.2}$$

and the same in ζ, on L_1 and L_2, with w an arbitrary point of the strip S, and λ a real parameter. Although the only admissible variations are

those which convert L_1 and L_2 into themselves in a monotonic continuous way, with preservation of the point at infinity, and the transformation (5.2) does not do this; still this variation is allowable, for $|\lambda|$ sufficiently small, as a combination of admissible variations [cf. Two Contours, pp. 332–334].

It is readily calculated that by (5.2) and the analogue in ζ, we have

$$\frac{dz'd\zeta'}{4\sinh^2\frac{1}{2}(z'-\zeta')} = \frac{dzd\zeta}{4\sinh^2\frac{1}{2}(z-\zeta)} - \lambda\frac{dzd\zeta}{16\sinh^2\frac{1}{2}(z-w)\sinh^2\frac{1}{2}(\zeta-w)} + \ldots, \quad (5.3)$$

the dots denoting terms in higher powers of λ.

The principal feature of the calculation is the use of the identity

$$\sinh^2\tfrac{1}{2}(z-w) + \sinh^2\tfrac{1}{2}(\zeta-w) - 2\sinh\tfrac{1}{2}(z-w)\sinh\tfrac{1}{2}(\zeta-w)\cosh\tfrac{1}{2}(z-\zeta) = \sinh^2\tfrac{1}{2}(z-\zeta), \quad (5.4)$$

which can be obtained by squaring the subtraction formula for sinh:

$$\sinh\tfrac{1}{2}(z-w)\cosh\tfrac{1}{2}(\zeta-w) - \cosh\tfrac{1}{2}(z-w)\sinh\tfrac{1}{2}(\zeta-w) = \sinh\tfrac{1}{2}(z-\zeta),$$

and making certain simple transformations, including the subtraction formula for cosh:

$$\cosh\tfrac{1}{2}(z-w)\cosh\tfrac{1}{2}(\zeta-w) - \sinh\tfrac{1}{2}(z-w)\sinh\tfrac{1}{2}(\zeta-w) = \cosh\tfrac{1}{2}(z-\zeta).$$

Multiplying (5.3) by

$$\sum_{i=1}^{n}[{}'g_{\alpha i}(z') - {}'g_{\beta i}(\zeta')]^2 = \sum_{i=1}^{n}[g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2,$$

and integrating, we get

$$A({}'g_1, {}'g_2) = A(g_1, g_2) - \lambda\cdot\frac{1}{4\pi}\sum_{\alpha\beta}\int_{L_\alpha}\int_{L_\beta}\sum_{i=1}^{n}[g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2 \frac{dzd\zeta}{16\sinh^2\frac{1}{2}(z-w)\sinh^2\frac{1}{2}(\zeta-w)} + \ldots. \quad (5.5)$$

If $(g_1, g_2) = (g_1^*, g_2^*)$, this function of λ has a minimum for $\lambda = 0$, and therefore the coefficient of the first power of λ vanishes:

$$\sum_{\alpha\beta}\int_{L_\alpha}\int_{L_\beta}\sum_{i=1}^{n}[g_{\alpha i}(z) - g_{\beta i}(\zeta)]^2\frac{dzd\zeta}{16\sinh^2\frac{1}{2}(z-w)\sinh^2\frac{1}{2}(\zeta-w)} = 0. \quad (5.6)$$

But, according to the formula (2.13), this is the same as

$$\sum_{i=1}^{n}F_i'^2(w) = 0. \quad (5.7)$$

6. *Conformal Mapping.*—Analogous to the author's previous work, the preceding theory gives for $n = 2$ the conformal mapping of any crescent-shaped plane region—i.e., one bounded by two Jordan curves with a unique point in common, one curve enclosing the other—on a circular crescent, including the continuous attachment of the conformal map to a topological correspondence between the boundaries.

[1] "The Problem of Plateau for Two Contours," *Jour. Math. Phys.*, **10**, 315–359 (1931). This paper will be cited as "Two Contours."

[2] "Solution of the Problem of Plateau," *Trans. Amer. Math. Soc.*, **33**, 263–321 (1931). This paper will be cited as "One Contour."

[3] One Contour, p. 282.

GROUPS GENERATED BY TWO OPERATORS OF ORDER 3 WHOSE COMMUTATOR IS OF ORDER 2

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Let s and t represent two operators of order 3 such that their commutator s^2t^2st is of order 2. It is known that then each of the four commutators whose elements are powers of s and t

$$s^2t^2st \qquad s^2tst^2 \qquad st^2s^2t \qquad sts^2t^2$$

is of order 2 and hence there result the following identities

$$s^2t^2st = t^2s^2ts,\ s^2tst^2 = ts^2t^2s,\ st^2s^2t = t^2sts^2,\ sts^2t^2 = tst^2s^2.$$

Since $t^2s^2ts \,.\, s^2tst^2 = t^2s^2t^2st^2$ and $t^2s^2t^2st^2 \,.\, t^2s^2t^2st^2 = t^2s^2t^2sts^2t^2st^2 = t^2s^2t^2 \,.\, tst^2s^2 \,.\, st^2 = 1$, it follows that the first and the second of these four commutators are commutative. Similarly it follows from the identities $s^2t^2st \,.\, t^2sts^2 = s^2t^2s^2ts^2$ and $s^2t^2s^2ts^2 \,.\, s^2t^2s^2ts^2 = s^2t^2s^2tst^2s^2ts^2 = s^2t^2s^2 \,.\, sts^2t^2 \,.\, ts^2 = 1$, that the first of these four commutators is also commutative with the third.

It seems desirable to employ a different method to prove that the first and fourth of these commutators are commutative but a similar method will be employed to prove that the fourth of these commutators is also commutative with the second and third, as follows: From the identities $s^2tst^2 \,.\, tst^2s^2 = s^2ts^2t^2s^2$, and $s^2ts^2t^2s^2 \,.\, s^2ts^2t^2s^2 = s^2ts^2t^2sts^2t^2s^2 = s^2t \,.\, t^2s^2ts \,.\, s^2t^2s^2 = 1$, it results that the second and the fourth are commutative. Similarly, the fact that the third and the fourth are commutative results from the identities $t^2sts^2 \,.\, sts^2t^2 = t^2st^2s^2t^2$ and $t^2st^2s^2t^2 \,.\, t^2st^2s^2t^2 = t^2st^2s^2tst^2s^2t^2 = t^2s \,.\, s^2t^2st \,.\, t^2s^2t^2 = 1$.

It has not yet been proved that the first and last of these four commu-

tators as well as the second and third, are commutative. Since these two pairs of operators are of order 2 they generate two dihedral groups. To prove that they are commutative it is only necessary to prove that the orders of these two dihedral groups cannot exceed 4. We shall first prove that these groups have the same order. The transform of the former of these groups by s is generated by the two operators $st^2sts = st^2s^2t \,.\, t^2s^2ts$ and ts^2t^2s. Since t^2s^2ts is commutative with each of these two generators it results that the dihedral group generated by them is simply isomorphic with the one generated by the second and the third of the given four commutators. That is, the two dihedral groups under consideration have a common order.

To prove that this common order cannot exceed 4 it should be noted that the four given commutators generate the commutator subgroup H of the group G generated by s and t, and that the two given dihedral groups are invariant subgroups of H. The transform of the former of these dihedral groups, as noted in the preceding paragraph, cannot be invariant under H unless t^2s^2ts is thus invariant. This is, however, possible only when the common order of these dihedral groups does not exceed 4. Hence it has been proved that each of the four given commutators is commutative with each of the others and hence the order of H cannot exceed 16 and the order of G cannot exceed 144.

In order to determine G it is therefore only necessary to construct a group of order 144 which is generated by two operators of order 3 whose commutator is of order 2. The direct product of two tetrahedral groups is obviously such a group and hence we have established the following theorem: *If two operators of order* 3 *have a commutator of order* 2 *but are not otherwise restricted they generate the direct product of two tetrahedral groups.*

It is now easy to determine all the possible groups which are generated separately by two operators of order 3 whose commutator is of order 2 since all such groups must be quotient groups of the direct product of two tetrahedral groups. Moreover, each of them must be non-abelian since two commutative operators of order 3 could not have a commutator of order 2. The smallest such group is therefore the tetrahedral group. This corresponds to the quotient group of G with respect to either of its two invariant subgroups of order 12. There are also two and only two invariant subgroups of order 4 in G and each of these gives rise to a quotient group which is simply isomorphic with the direct product of the tetrahedral group and the group of order 3. As G obviously contains no other invariant group besides the identity whose order is less than 12 it has been proved that *there are three and only three groups which can be separately generated by two operators of order* 3 *whose commutator is of order* 2. *These are the tetrahedral group, the direct product of the tetrahedral group and the group of order* 3, *and the direct product of two tetrahedral groups.*

It may be desirable to add that a simple method of constructing s and t so that they satisfy the given conditions and generate the direct product of two tetrahedral groups is as follows: Represent two tetrahedral groups on distinct sets of letters and construct the operators s and t so that each of them has a constituent from each of these two tetrahedral groups. The two constituents of s and t from one of these two tetrahedral groups appear in the same co-set of this group with respect to its invariant subgroup of order 4 while those from the other appear in two different such co-sets. Hence it results that both st and st^2 are of order 6 and that their squares are operators of order 3 in the two given tetrahedral groups.

Since the Sylow subgroups of order 9 in G are not invariant and do not involve any invariant subgroup of G besides the identity it is possible to represent G as a transitive permutation group of degree 16, and when it is thus represented its characteristic subgroup of order 16 will be regular. Hence G appears in the holomorph of the abelian group of order 16 and of type (1, 1, 1, 1), and corresponds to one of the 280 Sylow subgroups of order 9 in the group of isomorphisms of this abelian group. This holomorph was considered by the present writer in the *American Journal of Mathematics*, volume 20 (1898), page 229, and hence it results that we may take for s and t the following two permutations of this holomorph as it is there represented:

$$agc.bin.doj.fkl.hmp, \quad ajf.bhk.cdn.eog.ilp.$$

When G is represented according to the method noted in the preceding paragraph the operators s and t can be represented as permutations of degree 6. It is well known that when two operators of order 3 have a product of order 2 they must generate the tetrahedral group and hence it is of interest to note that the tetrahedral group plays such a fundamental rôle when their commutator is of order 2.

Whenever a group is determined by the orders of two operators and the order of their commutator it must have for a quotient group the abelian group which is the direct product of cyclic groups whose orders are the orders of these two operators. This results directly from the fact that to each of these two operators we can adjoin an operator of equal order which is commutative with the two operators without affecting their commutator. In particular, if a group is determined by two operators of order 2 and the order of their commutator it is dihedral and has the four group for a quotient group whenever this commutator is of even order and if it is determined by two operators which are restricted only by the facts that they are of order 3 and the order of their commutator is given it has the non-cyclic group of order 9 for a quotient group. If it is determined by two operators of orders 2 and 3, respectively, which are not further restricted except that the order of their commutator is given it

has the cyclic group of order 6 for a quotient group. If the order of this commutator is 2 it is known that the corresponding group is the direct product of the tetrahedral group and the group of order 2.

When G is determined by the two operators s and t of orders 2 and 3, respectively, which are not otherwise restricted except that the order of their commutator is 3 then there is no upper limit for the order of G, but all such groups are solvable since the commutator subgroup of the commutator subgroup must always be abelian. In fact, it is easy to verify that the commutator of $stst^2$ and t^2sts is then $(ts)^6$ while that of tst^2s and st^2st is $(st)^6$ and the product of these two commutators in order is $t(st^2)^6t^2$. As $(st)^6$ is commutative with this product it results that $(ts)^6$ and $(st)^6$ are commutative. This implies that the commutator subgroup of the commutator subgroup is abelian since it is obviously generated by these two sixth powers. If the order of st is assumed to divide 6 but no additional restrictions are imposed upon s and t then G is the group of order 54 obtained by extending the non-abelian group of order 27 which involves no operator whose order exceeds 3 by an operator s of order 2 under which it is invariant and which transforms into their inverses all the operators of one of its subgroups of order 9 and transforms an operator t of this group of order 27 but not found in this subgroup into itself multiplied by an operator contained therein but not invariant under this group of order 27^2.

It is easy to verify that $(st)^2$ is commutative with $(ts)^2$ in all the groups considered in the preceding paragraph and that these two operators generate an invariant subgroup of all of these groups. Hence this infinite system of groups may be constructed as follows: The direct product of two cyclic groups C_1, C_2 of the same arbitrary order is extended by an operator t of order 3 such that $t^2C_2t = C_1$, $t^2C_1C_2t = C_2^{-1}$, while s transforms C_1 into C_2, and t into $C_1.t^2$. The group generated by C_1, C_2 and t involves only operators of order 3 in addition to those of the direct product C_1 and C_2. This may be regarded as a direct generalization of the tetrahedral group. The entire group G may be regarded as a direct generalization of the octahedral group and involves one and only one subgroup of index 2. When C_1 is of order 2 there results the group of the cube and when C_1 is of order 3 there results the group of order 54 noted in the preceding paragraph.

[1] G. A. Miller, *Proc. Nat. Acad. Sci.*, **18**, 665 (1932).

[2] Cf. H. R. Brahana, *Am. Jour. Math.*, **50**, 347 (1928).

INTERPOLATION AND AN ANALOGUE OF THE LAURENT DEVELOPMENT

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In a recent note[1] the writer has pointed out the close analogy between approximation in the sense of least squares by polynomials on the unit circle $C: |z| = 1$ to an arbitrary function $f(z)$ continuous on C, and interpolation by polynomials in the nth roots of unity to this same function. We have the following two theorems:[2]

I. *Let $f(z)$ be analytic for $|z| \leqq R > 1$, let $P_n(z)$ denote the polynomial of degree n of best approximation to $f(z)$ on C in the sense of least squares [that is, $P_n(z)$ is the sum of the first $n+1$ terms of the Maclaurin development of $f(z)$], and let $p_n(z)$ denote the polynomial of degree n determined by interpolation to $f(z)$ in the $(n+1)$st roots of unity. Then we have*

$$\lim_{n\to\infty} p_n(z) = f(z), \text{ for } |z| < R, \text{ uniformly for } |z| \leqq R_1 < R. \quad (1)$$

Moreover we have

$$\lim_{n\to\infty} [P_n(z) - p_n(z)] = 0, \text{ for } |z| < R^2, \text{ uniformly for } |z| < R_1^2 < R^2. \quad (2)$$

It will be noted that many results concerning the convergence of the sequence $p_n(z)$ can be read off directly from (2)—Abel's theorem and its modified converse, divergence of the sequence $p_n(z)$ for $R < |z| < R^2$ if $f(z)$ has a singularity for $|z| = R$, etc.

An illuminating special case of the following is due to Méray; the general theorem is to be found in the reference:[1]

II. *Let $f(z)$ be continuous for $|z| = 1$ and let $p_n(z)$ denote the polynomial of degree n found by interpolation to $f(z)$ in the $(n+1)$ st roots of unity. Then we have*

$$\lim_{n\to\infty} p_n(z) = \frac{1}{2\pi i}\int_C \frac{f(t)dt}{t-z}, \text{ for } |z| < 1, \text{ uniformly for } |z| \leqq r < 1. \quad (3)$$

The right-hand member of (3) is also the limit for $|z| < 1$ of the sequence of polynomials $P_n(z)$ of degree n found by best approximation to $f(z)$ on C in the sense of least squares. If, however, a sequence of polynomials $P_n'(z)$ of degree n is found say by best approximation to $f(z)$ on C in the sense of Tchebycheff, then the limit of $P_n'(z)$ for $|z| < 1$ is not in general the right-hand member of (3).

It is the object of the present note to point out the close analogy *for expansions in rational functions* between interpolation in roots of unity and approximation on $C: |z| = 1$ in the sense of least squares. We prove the two following theorems, which correspond closely to I and II. These new theorems bear the relation to the Laurent series that I and II bear to the Taylor series.

III. *Let C denote the unit circle, $f(z)$ a function analytic for $1/R < |z| < R > 1$:*

$$\begin{aligned} f(z) &= f_1(z) + f_2(z), z \text{ on } C, \\ f_1(z) &= a_0 + a_1 z + a_2 z^2 + \ldots, \\ f_2(z) &= a_{-1} z^{-1} + a_{-2} z^{-2} + \ldots, \end{aligned} \tag{4}$$

and $r_{2n}(z)$ the function

$$\begin{aligned} r_{2n}(z) &= r_n'(z) + r_n''(z), \\ r_n'(z) &= a_{0n} + a_{1n} z + \ldots + a_{nn} z^n, \\ r_n''(z) &= a_{-1n} z^{-1} + a_{-2n} z^{-2} + \ldots + a_{-nn} z^{-n}, \end{aligned} \tag{5}$$

which coincides with $f(z)$ in $2n + 1$ points equally spaced on C. Then we have

$$f(z) = \lim_{n \to \infty} r_{2n}(z), \text{ for } 1/R < |z| < R, \text{ uniformly for } 1/R_1 \leqq |z| \leqq R_1 < R$$
$$f_1(z) = \lim_{n \to \infty} r_n'(z), \text{ for } |z| < R, \text{ uniformly for } |z| \leqq R_1 < R,$$
$$f_2(z) = \lim_{n \to \infty} r_n''(z), \text{ for } |z| > 1/R, \text{ uniformly for } |z| \geqq 1/R_1 > 1/R.$$

IV. *Let C denote the unit circle and $f(z)$ a function continuous on C. Introduce the notation*

$$\begin{aligned} f_1(z) &= \frac{1}{2\pi i} \int_C \frac{f(t)dt}{t - z}, \quad |z| < 1, \\ f_2(z) &= \frac{1}{2\pi i} \int_C \frac{f(t)dt}{t - z}, \quad |z| > 1, \end{aligned} \tag{6}$$

If $f(z)$ in (4) is the formal Laurent expansion of $f(z)$ on C, then the representations (4) and (6) of $f_1(z)$ for $|z| < 1$ and of $f_2(z)$ for $|z| > 1$ are known to agree. If now $r_{2n}(z)$ denotes the function as in (5) which coincides with $f(z)$ in the $(2n + 1)$st roots of unity, then we have

$$\begin{aligned} f_1(z) &= \lim_{n \to \infty} r_n'(z), \text{ for } |z| < 1, \text{ uniformly for } |z| \leqq r < 1, \\ f_2(z) &= \lim_{n \to \infty} r_n''(z), \text{ for } |z| > 1, \text{ uniformly for } |z| \geqq R > 1. \end{aligned} \tag{7}$$

In (6) the second integral is to be taken in the positive sense with respect to the region $|z| > 1$, that is, in the clockwise sense on C.

Let us give first a proof of IV, using direct methods; this proof is similar to the proof of II (loc. cit.).

Introduce the notation

$$\omega = e^{2\pi i/(2n+1)}.$$

Then, since $r_{2n}(z)$ is found by interpolation to $f(z)$ in the $2n+1$ distinct points ω^k, the function $z^n r_{2n}(z)$ is a polynomial in z of degree $2n$ defined by interpolation to the function $z^n f(z)$ in the points ω^k, and is represented by Lagrange's interpolation formula. Lagrange's formula for the polynomial $p_m(z)$ of degree m which takes on the values $K_1, K_2, \ldots, K_{m+1}$ in the $m+1$ distinct points $z_1, z_2, \ldots, z_{m+1}$ is

$$p_m(z) = \sum_{k=1}^{m+1} \frac{K_k}{p'(z_k)} \frac{p(z)}{z - z_k},$$

where $p(z) = (z - z_1)(z - z_2)\ldots(z - z_{m+1})$; the polynomial $p_m(z)$ is uniquely determined by these requirements. Under the circumstances of the present theorem we have

$$z^n r_{2n}(z) = \sum_{k=1}^{2n+1} f(\omega^k)\omega^{kn} \frac{\omega^k(z^{2n+1} - 1)}{(2n+1)(z - \omega^k)},$$

$$r_{2n}(z) = \frac{z^{2n+1} - 1}{(2n+1)z^n} \sum_{k=1}^{2n+1} \frac{f(\omega^k)\omega^{k(n+1)}}{z - \omega^k}.$$

We find $r_n'(z)$ by omitting here the negative powers of z. Clearly one has

$$\frac{z^{2n+1} - 1}{z^n(z - \omega^k)} = z^n + \omega^k z^{n-1} + \omega^{2k} z^{n-2} + \ldots + \omega^{2nk} z^{-n},$$

from which the non-negative powers of z are

$$z^n + \omega^k z^{n-1} + \ldots + \omega^{nk} = \frac{z^{n+1} - \omega^{k(n+1)}}{z - \omega^k}.$$

This yields

$$r_n'(z) = \sum_{k=1}^{2n+1} \frac{f(\omega^k)\omega^{k(n+1)}(z^{n+1} - \omega^{k(n+1)})}{(2n+1)(z - \omega^k)}.$$

The expression on the right suggests the computation of $f_1(z)$ directly by means of the definite integral in (6), where the circumference C is divided into $2n+1$ parts by the points ω^k:

$$f_1(z) = \lim_{n \to \infty} \frac{1}{2\pi i} \sum_{k=1}^{2n+1} \frac{f(\omega^k)(\omega^{k+1} - \omega^k)}{\omega^k - z}, \quad |z| < 1; \tag{8}$$

the limit on the right exists uniformly[3] for all $|z| \leqq r < 1$.

We find now

$$\lim_{n \to \infty} [f_1(z) - r_n'(z)] = \lim_{n \to \infty} \sum_{k=1}^{2n+1} \left[\frac{1}{2\pi i} + \frac{\omega^{nk} z^{n+1} - 1}{(2n+1)(\omega - 1)}\right] \frac{\omega^k(\omega - 1)f(\omega^k)}{\omega^k - z}. \tag{9}$$

The quantity $(2n + 1)(\omega - 1)$ approaches as its limit $2\pi i$, for we have

$$\omega = \cos \frac{2\pi}{2n+1} + i \sin \frac{2\pi}{2n+1},$$

$$\frac{(2n+1)(\omega-1)}{2\pi i} = \frac{\cos \dfrac{2\pi}{2n+1} - 1}{\dfrac{2\pi i}{2n+1}} + \frac{\sin \dfrac{2\pi}{2n+1}}{\dfrac{2\pi}{2n+1}},$$

which approaches the limit unity. By the uniformity of the convergence in (8) as applied to the right-hand member of (9) and also by the uniform convergence to zero of z^{n+1} for $|z| \leqq r < 1$, we have now the first of the equations (7).

We omit the details of the proof of the second of equations (7), for they are similar to the details already given.

It will be noted that in IV as in II the given function $f(z)$ need not be continuous on C provided it is integrable on C in the sense of Riemann.

Let us turn now to the proof of III. A proof can readily be given by the direct study of the functions involved, as suggested by the proof of IV just presented. A shorter proof of III is, however, the following.

If $R_2 < R$ is arbitrary, there exists M such that

$$\left| f(z) - [a_{-n}z^{-n} + a_{-n+1}z^{-n+1} + \ldots + a_0 + a_1 z + \ldots + a_n z^n] \right| \leqq \frac{M}{R_2^n}, \; z \text{ on } C; \quad (10)$$

the proof is immediate by the Cauchy inequality for the coefficients a_k as applied to $f_1(z)$ and $f_2(z)$. It will be noticed that the polynomial in z and $1/z$ which appears in (10) is a trigonometric polynomial of order n.

From (10) follows now from a very general theorem due to Jackson[4] the inequality

$$\left| f(z) - r_{2n}(z) \right| \leqq \frac{2BM \log n}{R_2^n}, \; z \text{ on } C,$$

where B is an absolute constant. The conclusion of III is an immediate consequence of a theorem due to the present writer.[5]

One might suspect by analogy with I that in III the equation

$$\lim_{n \to \infty} [r_n'(z) - (a_0 + a_1 z + \ldots + a_n z^n)] = 0$$

could be established for certain values of z in modulus greater than R, at least in case $f(z)$ has no singularity for $|z| \geqq R$. That is not the case, however, for an arbitrary function $f(z)$, as we proceed to show by an example.

Choose $f(z) = 1/(z - \rho)$, $0 < \rho < 1$. We find in succession the equations (which may be verified directly)

$$\frac{z^n}{z - \rho} - z^n r_{2n}(z) = \frac{\rho^n(z^{2n+1} - 1)}{(\rho^{2n+1} - 1)(z - \rho)},$$

$$r_{2n}(z) = \frac{(\rho^{2n+1} - 1)z^n - \rho^n(z^{2n+1} - 1)}{(\rho^{2n+1} - 1)(z - \rho)z^n},$$

$$r_n'(z) = -\frac{\rho^n(z^n - \rho^n)}{(\rho^{2n+1} - 1)(z - \rho)}$$

We also find

$$a_0 + a_1 z + \ldots + a_n z^n = 0,$$

$$r_k'(z) - (a_0 + a_1 z + \ldots + a_n z^n) = -\frac{\rho^n(z^n - \rho^n)}{(\rho^{2n+1} - 1)(z - \rho)};$$

this right-hand member approaches zero ($|z| > 1$) if and only if we have $|z| < 1/\rho$.

The writer is not aware of any illustration other than $r_{2n}(z)$ of a sequence of functions found by interpolation *in a multiply-connected region* from an arbitrary function analytic in that region, which represents in that multiply-connected region the given analytic function.

[1] *Bull. Amer. Math. Soc.*, **38**, 289–294 (1932).

[2] I is due to Runge, *Theorie und Praxis der Reihen*, p. 137 (1904); Fejér. Göttinger Nachrichten, 319–331 (1918); (see also Kalmár, *Mathematikai és Physikai Lapok*, 120–149 (1926)); and Walsh, *Trans. Amer. Math. Soc.*, **34**, 22–74 (1932).

[3] Runge, *Acta Math.*, **6**, 229–244 (1885); Montel, *Séries de polynomes*, 51 (1910); or Osgood, *Funktionentheorie*, 579–581 (1928).

[4] *The Theory of Approximation* (1930), p. 121 Theorem I. To be sure, Jackson's theorem is there stated merely for real functions but follows immediately in the more general case.

[5] *Trans. Amer. Math. Soc.*, **30**, 838–847 (1928), Theorem II. Compare also de la Vallée Poussin, *Approximation des Fonctions*, Ch. VIII (1919), who does not bring out clearly however the convergence of the sequences $r_{2n}(z)$, $r_n'(z)$, $r_n''(z)$ as expressed in III.